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"Grassland in a jar" – an ecological view of the archaeobotanical contents of vessels from two Lusatian Urnfield Culture settlements (Early Iron Age) in north-central Poland

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ABSTRACT. During the archaeological exploration of two Lusatian Urnfield Culture settlements, dated to the Early Iron Age and located in north-central Poland, 11 well-preserved clay vessels filled with waterlogged botanical remains were discovered. Their position and context led archaeologists to suggest a possible function of these vessels as foundation offerings. Accordingly, the results of archaeobotanical analyses were discussed within this context. The qualitative and quantitative richness of the subfossil samples collected from these vessels also offered an opportunity to provide data on the vegetation that developed in the vicinity of both settlements. This study focuses on grassland vegetation as a contribution to the broader history of grasslands in different European regions. The potential and limitations of reconstructing ancient vegetation and land use from archaeobotanical material of complex origin are also discussed.

KEYWORDS: archaeobotany, botanical vessel fillings, history of meadows and pastures, landscape transformation, foundation offering, Lusatian Urnfield Culture

INTRODUCTION

The history of grasslands is a subject of interest that unites several scientific disciplines and requires extensive interdisciplinary cooperation to address issues relevant to each field. For botanists and ecologists studying processes in modern grassland communities, knowledge of their origin and long-term dynamics under changing climate conditions and land-use practices is of paramount importance. According to Poschlod (2015), preserving and maintaining grassland biodiversity requires understanding both the historical and current contexts. There are also several reasons why knowledge of grassland history is essential for archaeology and related natural sciences such as archaeobotany and archaeozoology. Forests, open wetlands, and patches of other herbaceous vegetation within woodlands have always been important to humans as a source of food, medicinal plants, and raw materials for various purposes, as well as fodder for grazing game and later domestic animals

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(Kubiak-Martens, 1996, 2002; Bishop et al., 2015; Divišová and Šida, 2015). The development of a sedentary lifestyle and agriculture by Neolithic tribes initiated regular thinning of forests through burning, logging and cattle grazing, which gradually increased the area of semi-open and then open pastures, cultivated fields, and settlements (Noryśkiewicz, 2013; Woodbridge et al., 2014; Jacomet et al., 2016; Czerniak et al., 2023). In subsequent periods, cultural development was combined with innovations in agricultural management tools and methods, including those related to animal husbandry (Urban, 2019; Hald et al., 2024). The area used for pastures and meadows, the length of the grazing season, and the quality of fodder intended for livestock were all important for the subsistence economy, which affected human well-being and demographic processes. Therefore, the history of grasslands (pastures and meadows) in a given area coincides with the regional history of civilization.

Natural wetlands and semi-natural grasslands are of special scientific interest as endangered ecosystems in many regions of the world (Middleton et al., 2006; Habel et al., 2013; Davidson, 2014). In Europe, fen meadows receive particular attention as biodiversity hotspots and home for many endangered species; however, they have experienced significant decline due to sensitivity to environmental changes and management practices (Stammel et al., 2003; Biró et al., 2020; Kulik et al., 2023; Reutimann et al., 2023). Other grassland ecosystems are also declining, threatening many rare and specialist species of flora and fauna, which calls for their urgent protection (Söderström et al., 2001; Cremene et al., 2005; Pärtel et al., 2005; Janišová et al., 2011; Ozinga et al., 2013). These processes are progressing because of the climate warming negative effects on water balance in soil, and due to various forms of human impact including drainage, conversion into arable land, animal husbandry (overgrazing) and then industrial and residential uses. An increasing number of studies focus on undesirable changes in seminatural grasslands due to the modern socioeconomic transformations of rural areas. Intensification of livestock production has shifted from extensive grazing on pastures to housing animals in confined spaces and feeding them formulated diets. The practice of sowing specific grass seeds and using artificial fertilizers aims to produce highly nutritious fodder, and hay harvesting has changed due to modern specialized equipment. These 20th-century agricultural innovations have strongly affected meadow ecosystems through floristic impoverishment. Furthermore, reduced demand for open pastures and traditionally managed meadows has led to their gradual abandonment and transformation, favoring the spread of highly competitive, invasive tall forbs and grasses, followed by overgrowth by shrubs and trees. This succession results in further loss of plant species richness and diversity, as well as the specific character and functioning of these ecosystems (Cremene et al., 2005; Poschlod et al., 2005; Habel et al., 2013; Bonari et al., 2017; Swacha et al., 2018; Valkó et al., 2018).

Recently, the observed decline and degradation of grasslands have become a subject of thorough debate concerning the loss of a broad range of so-called "ecosystem services," including some economic benefits previously underestimated (Maltby and Acreman, 2011; Bonari et al., 2017; Hanisch et al., 2020; Grange et al., 2021). Therefore, this discussion also concerns grassland conservation and restoration methods (Stammel et al., 2003; Middleton et al., 2006; Tälle et al., 2016, 2018). Both experimental studies and classical research are used to elucidate successional processes and the role of functional traits of leading and diagnostic species under different types and intensities of management (burning, mowing, livestock grazing, abandonment) as tools for grassland restoration (Moog et al., 2002; Kahmen and Poschlod, 2008; Milberg et al., 2018; Swacha et al., 2018, 2023; Sienkiewicz-Paderewska et al., 2020). This creates a need for a better understanding of wetlands and other types of grassland functioning and ecology, as well as their long-term history in the context of natural and anthropogenic impacts (Pärtel et al., 2005; Hejcman et al., 2013; Eriksson and Cousins, 2014; Poschlod, 2015; Feurdean et al., 2018).

Plant remains are the main direct material evidence used in discussions on the history of grasslands. They document the presence of particular species in specific areas and times, while knowledge of their ecological requirements (Ellenberg et al., 1992; Zarzycki et al., 2002), functional traits (Klimešová et al., 2008; Ladouceur et al., 2019; Lengyel et al., 2020), and co-occurrence with other species in recent plant communities (Ellenberg et al., 1992;

Matuszkiewicz, 2001) serves to reconstruct potential past vegetation and agricultural management methods (Hodgson et al., 1999; Lodwick, 2017). In general, the interpretation of archaeobotanical data for reconstructing past plant community composition faces several constraints, not only due to the fragmentary nature of such materials and their usually complex origin, but also because of limitations in using modern vegetation data for this purpose. When searching for potential analogs of ancient plant communities in present-day vegetation, numerous natural and anthropogenic factors that have shaped their development over thousands of years must be considered (Behre and Jacomet, 1991; Lityńska-Zając and Wasylikowa, 2005). Moreover, due to the recent rapid decline of earlier grassland communities (Sucholas et al., 2022), especially in the densely settled lowlands of Central Europe, it is virtually impossible to find patches of meadows and pastures resembling those used in historic and prehistoric times.

Although the long-term history of grasslands is the subject of a growing number of studies (Pärtel et al., 2005; Poschlod et al., 2009; Hejcman et al., 2013; Kuneš et al., 2015; Poschlod, 2015; Feurdean et al., 2018), original palaeobotanical data providing information on the occurrence of specific grassland species assemblages in different periods and regions of Europe still need to be supplemented. Pollen data cover almost the entire European area (European Pollen Database 2007–2025), enabling estimations of forest-open land dynamics at various spatial and temporal scales (Ralska-Jasiewiczowa et al., 2004; Nielsen et al., 2012; Fyfe et al., 2015; Jamrichová et al., 2017; Pędziszewska et al., 2020) and allowing reconstruction of general land-use history trends in particular regions (Berglund, 1991; Abraham et al., 2016; Kozáková et al., 2021; Vinogradova et al., 2023). However, pollen data alone usually do not allow for a detailed characterization of grassland ecosystems. In contrast, well-preserved plant macrofossils make it possible to identify some elements of the species composition of past vegetation at a given site and its surroundings and may provide insights into farming methods (Körber-Grohne et al., 1983; Hodgson et al., 1999; Lodwick, 2017; Akeret et al., 2018; Maciejewska et al., 2022; Šálková et al., 2022; Jakobitsch et al., 2023). Studies combining pollen and macrofossil data or relying on large macrofossil datasets focusing on grassland history or considering this issue in detail, remain infrequent and unevenly distributed across European regions and periods (but see e.g. Greig, 1988; Knörzer, 1996; Pokorná et al., 2018). In this respect, one of the most interesting and poorly studied periods in northern Central Europe is the Late Bronze and Early Iron Age transition. So far, archaeobotanical records for this period mostly concern cultivated plants, with few source materials illustrating the vegetation of settlement hinterlands.

The Late Bronze Age to Early Iron Age transition was a period of important socioeconomic transformations that occurred under conditions of a marked climate change in the Northern Hemisphere (Beer and Van Geel, 2008; Turney et al., 2016; Bevan et al., 2017; Park et al., 2019). Archaeological data indicate that during this time, a large part of Central Europe (including most of modern Poland, eastern part of Germany, and some territories of Czech Republic, and Slovakia) was settled by population of the Lusatian Urnfield Culture (LUC) (Dąbrowski, 2009; Kaczmarek, 2017). Among the important determinants of this culture are characteristic funeral rites (cremation, characteristic urns, flat graveyards) and numerous defensive settlements (strongholds) (Dąbrowski, 2009; Góralczyk, 2024), as well as notable economic strategies (Kaczmarek, 2017; Urban, 2019). Settlements were often located near lake shores, on lake islands, or on lower terraces above floodplains (i.e. in areas primarily covered by wetlands, which may have been used for livestock grazing). Numerous pollen diagrams illustrate a distinct increase in open land with a rising share of plant taxa typical for meadows and pastures in various habitats, such as *Plantago lanceolata*, *P. media*, Poaceae, *Rumex acetosa*-type, *Filipendula*, *Centaurea jacea*-type, *Ranunculus acris*-type and *Aster*-type, among others (Latałowa, 1982, 1992; Ralska-Jasiewiczowa and Van Geel, 1998; Niewiarowski and Noryśkiewicz, 1999; Makohonienko, 2000; Filbrandt-Czaja, 2009; Noryśkiewicz, 2013; Pędziszewska and Latałowa, 2016; Kołaczek et al., 2025). However, despite the relatively large number of LUC sites excavated in Poland (Urban, 2019; Góralczyk, 2024), archaeobotanical data so far mainly concern fragments of charred wood and diaspores of cultivated plants and field/ruderal weeds (Lityńska-Zając, 2005; Urban, 2019), while information related to other ecosystems remains very limited. The early work at the Biskupin stronghold (Gniezno Lakeland) by Jaroń (1938) still provides the best evidence of wild plants, including those likely to have grown in meadows and pastures surrounding this site. At other sites, as for example Sobiejuchy (Palmer, 2004), Grzybiany (Sady, 2015), and many more, macrofossil analyses revealed only a few taxa typical of this kind of vegetation.

During excavations of cultural layers at two LUC sites in north-central Poland – Polanowo and Mirakowo-Grodno – well-preserved clay vessels filled with waterlogged botanical remains were discovered (Gackowski, 2003; Pydyn, 2010). So far, the results of archaeobotanical analyses have mainly focused on the potential origin of the vessel fillings (Latałowa and Pińska, 2010) and plant use (Kunicka, 2012). However, the extensive lists of wild taxa found in the vessels also offer an opportunity to characterize elements of the vegetation that spread around both sites during the Early Iron Age. The main purpose of the present study is to provide new data on the floristic elements of vegetation that developed in the area occupied by the LUC population in north-central Poland, with special reference to grassland vegetation, as a contribution to grassland history in different European regions. Our objectives are also to illustrate and discuss the following:

– the potentials and limitations of reconstructing ancient vegetation from archaeobotanical material of complex origin, as reflected by our data,

– the potentials and limitations of such materials for reconstructing ancient land-use methods,

– the potential of the vessel fillings from Polanowo to be part of a ritual foundation offering.

ENVIRONMENTAL SETTINGS

Both study sites are in north-central Poland within the Central European Lowlands (Fig. 1). The topography and youngest geological structures of the area were shaped during

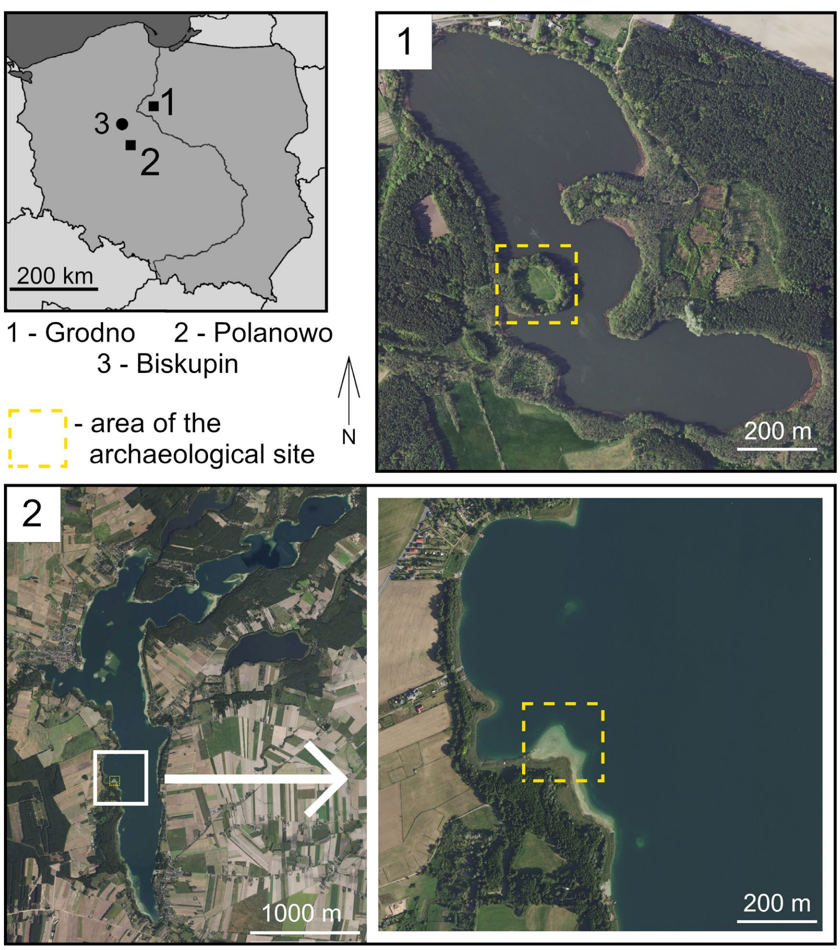

Figure 1. Location of the archaeological sites: Grodno and Polanowo. Available from www.geoportal.gov.pl. Accessed September 2022

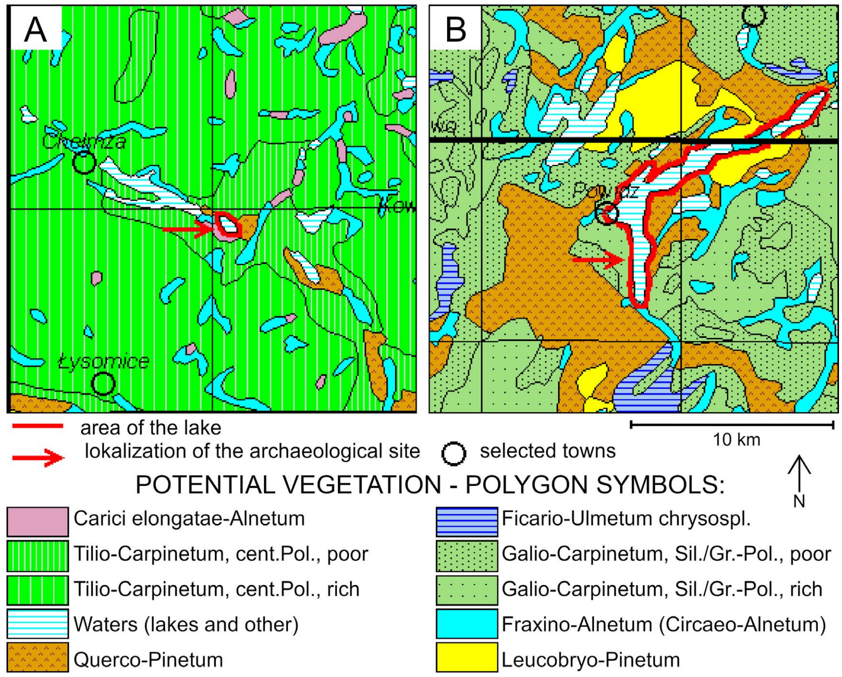

Figure 2. Potential natural vegetation map of the area around the Grodno and Polanowo sites (Matuszkiewicz, 2008, modified)

the last glaciation (Kondracki, 2012). The ice sheet and its meltwaters left terminal and ground moraine hills, mostly undulating and dissected by a dense hydrological network of interconnected lake channels and river valleys. Patches of outwash plains and kames were also formed. The area lies in the temperate climate zone, at the transition where Atlantic and continental air masses meet. The climate is relatively warm and dry, with an annual mean temperature between 8.0 and 9°C and average annual precipitation of ≤500 mm in the Gniezno Lakeland and between 500 and 600 mm in the Chełmno Lakeland. The mean temperature in January ranges from −2 to 0°C, while that in July is ~19°C (Klimat IMGW-PIB 2025). The growing season lasts between 219 and 238 days (Tomczyk and Szyga-Pluta, 2019), and the mean snow cover duration is ~40 days (Tomczyk et al., 2021). This area lies within the temperate deciduous forest biome.

The Polanowo site (17°55′59.1″E, 52°23′25.2″N) is situated on the western shore of Lake Powidzkie (Gniezno Lakeland, Wielkopolska region) (Fig. 1). It is a large channel lake, covering 1084 ha with a maximum depth of 47 m (approximately 11.5 m on average) and a long, highly diversified shoreline (Nowak et al., 2019a). During the Holocene, the lake basin underwent multiple hydrographic transformations caused by climate change, sediment accumulation, shifts in vegetation belts, and human activity (Nowak et al., 2019b). The lake's catchment contains a variety of soils. Rusty and podzolic soils developed on sandy substrates, while patches of more fertile brown and chestnut soils originate from sandy clay formations. Large lake channels and river valleys are filled with peaty soils (Nowak, 2019). The map of potential natural vegetation (Fig. 2) indicates that habitats of Central European oak-hornbeam forest (*Galio-Carpinetum*) and mesotrophic oak-pine forest (*Querco-Pinetum*) should co-dominate in the area. Within a few kilometers, large patches of habitats of poor pine forest (*Leucobryo-Pinetum*) also occur. Potential habitats of ash-alder riparian forest (*Fraxino-Alnetum*) and hardwood floodplain forest (*Ficario-Ulmetum*) are scattered throughout the area, some distance from the study site. According to the current vegetation survey (Chmiel et al., 2019), the present landscape is dominated by arable fields, grasslands and planted pine stands, but patches of forest communities growing in their original habitats, consistent with the potential vegetation map, have also been documented. Interestingly, the authors identified relatively large fragments of the thermophilous oak forest *Potentillo albae-Quercetum*, a forest community currently under threat, and which is expected to transform into an oak-hornbeam forest, if not active protection is applied (Kwiatkowska and Wyszomirski, 1988). *Potentillo albae-Quercetum* is characterized by a tall, transparent canopy; due to the spacing of oaks, abundant light reaches the ground, allowing light-demanding plants to dominate the herb layer. Among these, several rare and protected species typical for dry grasslands (*Festuco-Brometea*) find their habitats there, which is also true in the study area. Wetland and dry ground grasslands represent a wide range of plant communities, which, due to abandonment and negative changes in hydrological conditions, are subject to degradation. The presence of thermophilous swards and communities of tall herbs developing mainly along forest edges is a characteristic feature of the local vegetation (Chmiel et al., 2019).

The Mirakowo-Grodno site (Grodno in the following text) (53°09′30.5″N, 18°42′17.2″E) is situated on a peninsula on the western shore of Lake Grodzieńskie in the Chełmno Lakeland (Fig. 1). The lake covers 46 ha with a maximum depth of 7 m (3 m on average), and its shoreline is highly diversified. It occupies a small part of a long channel filled by larger lakes and wetlands. Flat and undulating moraine plains dominate the landscape, but a small patch of sandy outwash plain occurs near the lake. Leached brown soils dominate the area surrounding the lake, while peaty soils have developed in wetlands (Niewiarowski and Kot, 2010). The potential vegetation map (Fig. 2) indicates that, considering the potential of the habitats, the area is rather uniform and suggests oak-hornbeam forest (*Tilio-Carpinetum*) as the main vegetation type. Small, scattered patches of habitats of mesotrophic oak-pine forest (*Querco-Pinetum*), alder-ash riparian forest (*Fraxino-Alnetum*) and alder carr (*Carici elongatae-Alnetum*) are also present. Today, the area is strongly transformed by human activity and is mostly covered by fields, but large patches of forested land remain in the immediate surroundings of the lake. The largest woodland areas consist of pine plantations, other woods represent different variants of oak-hornbeam forest (*Tilio-Carpinetum*), small patches of riparian forest (*Fraxino-Alnetum*) and alder carr (*Carici elongatae-Alnetum*).

ARCHAEOLOGICAL CONTEXT OF THE STUDY

Polanowo is an underwater archaeological site dated to the Early Iron Age (radiocarbon dating range: 785–530 cal. years BCE; medians 670–635 cal. years BCE) (Pydyn and Rembisz, 2010) and identified as an open settlement from the late phase of the LUC (Pydyn, 2010). The distribution of numerous wooden structures and the lake's bottom topography suggest that the settlement occupied a small promontory now covered by water. High dispersion of the structures and other objects is likely the result of intensive wave and ice action along the shoreline, which is not surprising in such a large lake. Lithological, macrofossil and pollen analyses indicated disrupted, fragmented sediments at the site (Święta-Musznicka et al., 2010). More than half of the one-meter profile consisted of strongly consolidated, mostly mineral sediments of Late Glacial age, while the upper part of the profile (approximately 40 cm) was composed of calcareous gyttja with a high admixture of plant and animal detritus, dated to the late Holocene. The pollen and macrofossil data provided no evidence of local human activity, leading to the conclusion that the upper part of the sediments does not originate from the period of the settlement's functioning.

Settlement activity at the site is indicated not only by the remains of wooden constructions but also by the presence of querns, loom weights, metal objects, animal bones and abundant ceramics (Gręzak, 2010; Rembisz, 2010). Among these, two ceramic vessels with excellently preserved organic fillings were discovered. The first vessel (P10) was located close to wooden elements of a house and contained cattle limb bones, ceramic fragments and organic matter, which is the subject of the present study. The second vessel (P11), found in the same archaeological layer near another wooden construction, contained a cattle wrist bone and organic matter analysed in this study (Gręzak, 2010). It has been hypothesized that both vessels may have served as foundation offerings (Latałowa and Pińska, 2010; Pydyn and Rembisz, 2010).

The Grodno archaeological site is a stronghold (defence settlement) dated by dendrochronology to 776–684 years BCE and, based on the characteristics of the artifacts, identified as an LUC site (Gackowski, 2016). The stronghold is situated on a peninsula on Lake Grodzieńskie, which in the past may have been a sizeable island, several dozen meters from the former lakeshore. The island was still present at the end of the 18th century, but the gap between it and the shore was later filled in (Gackowski, 2009). An important part of the site consists of well-preserved wooden structures: a bridge connecting the island with the shore, an entrance gate, a palisade and buildings. A set of complete ceramic vessels with organic fillings was found at the palisade and bridge constructions (Gackowski, 2009, 2010). These were amphoras with pairs of handles, typically used as containers for liquids or loose products. The vessels were mostly undamaged and found standing upright. Similar to Polanowo, these vessels may have been part of a foundation offering (Gackowski, 2010).

MATERIAL AND METHODS

This study is based on previously published (Latałowa and Pińska, 2010), unpublished (Kunicka, 2012), and new results of archaeobotanical analyses of 11 vessel fillings containing organic waterlogged material: two from Polanowo and nine from Grodno (Table 1). All samples were collected by archaeologists during excavations and then delivered fresh to the archaeobotanical laboratory at the University of Gdańsk. The samples were taken from bottoms of the vessels, below thick layers of mineral lake sediments filling their upper parts. The standard procedure for preparing plant macroremains included soaking in a dilute potassium hydroxide solution for 24 hours; samples were then rinsed on three sieves (0.2, 0.5 and 2.8 mm). Seeds, fruits and other remains were separated under 16× magnification and stored in a preservative mixture of water, ethanol and glycerin (1:1:1) with a few thymol crystals. Identifications were made using specific keys and atlases (e.g. Kowal, 1953; Marek, 1954; Körber-Grohne, 1991; Cappers et al., 2012) and confirmed with modern specimens from the reference carpological collection (CRefColl-UGDA) in the Laboratory of Palaeoecology and Archaeobotany, Department of Plant Ecology, Faculty of Biology, University of Gdańsk.

Botanical nomenclature follows Mirek et al. (2020). In this study, the general term “grassland” refers to both natural and semi-natural vegetation dominated by herbaceous plants, if not specified as pasture (grazed grassland) or meadow (cut or mown grassland).

The full results of the archaeobotanical analysis, including taxa from various vegetation types, are provided in the supplementary material (Supplementary File 1[1]). The separate column in this table contains supplementary data of taxa identified in cultural layers of the LUC fortified settlement in Biskupin (Jaroń, 1938; Niezabitowski, 1938; Moldenhawer, 1948). The close geographical location of Biskupin to our sites (Gniezno Lakeland) and dendrochronological dating of its constructions to 747–722 BCE (Ważny, 2009) make these data useful even if, due to the lack of information on sample volumes, we provide only presence/absence data. All taxa were assigned to five ecosociological groups following ecological and habitat characteristics by Zarzycki et al. (2002), Roo-Zielińska (2014) and Mucina et al. (2016): (1) plants associated with meadows, pastures and other grasslands; (2) wetland plants; (3) plants associated with forests and forest edges; (4) ruderal and segetal plants; (5) cultivated plants. Taxa that could not be classified into these five groups were placed in an additional category – other taxa.

Taxa related to grasslands (including wetlands), which are the main subject of this study, are presented in Table 2. The basic interpretation of these results considers the occurrence of taxa in recent plant communities, with special reference to species characteristic of higher ranks (classes, orders) in phytosociological classifications (Matuszkiewicz, 2001; Mucina et al., 2016; Willner et al,. 2019; Kącki et al., 2020; Chytrý et al., 2024; FloraVeg.EU). To reduce potential bias due to the location of the study vessels within wetland vegetation, data related to wetland grasslands are analysed separately. Ecological and habitat characteristics follow Zarzycki et al. (2002), Roo-Zielińska (2014) Mucina et al. (2016). Ecological indices of edaphic factors used in the analyses follow the Polish version of indicator values (Zarzycki et al., 2002). Taxa with preferences in two indicator numbers were included in both groups, while those with broader ecological requirements were excluded from the analysis.

To illustrate similarities and differences among study samples regarding their botanical composition of grassland taxa, statistical analyses were conducted using CANOCO and CanoDraw 3.0 for Windows 4.5. All analyses were performed after square root transformation of the dataset. Based on the results of the preliminary detrended correspondence analysis (DCA) and considering the length of gradients (2–3), principal component analysis (PCA) was applied (Lepš and Šmilauer, 2003).

RESULTS

FLORISTIC COMPOSITION OF THE VESSEL INFILLS

The individual samples vary in volume (Table 1). In total, over 14000 seeds and fruits were found (more than 7500 in Grodno and over 6500 in Polanowo). Sample P10 from Polanowo was the richest in plant remains, despite not having the largest volume (Table 1; Fig. 3). A characteristic feature of the material from both sites was the large proportion of seeds from the Chenopodiaceae family (e.g. *Chenopodium album*, *Ch. ficifolium*, *Chenopodium* sp., *Atriplex* sp./*Chenopodium* sp.). Seeds of *Ch. album* are particularly numerous in sample P10, accounting for over 45% of all remains. In Grodno, seeds of Chenopodiaceae comprised more than 46% of all remains in samples. Identification of subfossil remains

[1] Supplementary File 1: List of all plant taxa identified in samples from the Polanowo and Grodno archaeological sites.

Table 1. List of samples included in the study

Sample code	Collection place	Sample volume (cm^3)	Sources
GRODNO			
G1	trench 16/10	15	Maciejewska and Badura, unpublished
G2	trench 18/10	300	Maciejewska and Badura, unpublished
G3	trench 18/10	300	Maciejewska and Badura, unpublished
G4	trench 16/10	300	Maciejewska and Badura, unpublished
G5	trench 16/10	200	Kunicka, 2012; Badura unpublished
G6	trench 16/10	25	Kunicka, 2012; Badura unpublished
G7	trench 16/10	200	Kunicka, 2012; Badura unpublished
G8	trench 16/10	300	Kunicka, 2012; Badura unpublished
G9	trench 16/10	580	Kunicka, 2012; Badura unpublished
POLANOWO			
P10	layer III (1EG/IV)	350	Latałowa and Pińska, 2010
P11	layer III (2EG/IV)	200	Latałowa and Pińska, 2010

distinguished over 200 plant taxa, including more than 170 species, assigned to five main ecological groups (ESM1). Again, the P10 sample from Polanowo differs in species composition from other samples, containing over 30 taxa not found in any other sample.

The highest number of taxa (73, including 70 species) represents various types of grasslands (Group 1), with 51 taxa (50 species) recorded in Polanowo and 49 taxa (46 species) in Grodno. Twenty-seven taxa are common to both sites; 24 are found exclusively in Polanowo, and 22 are found exclusively in Grodno. Among the taxa common to both sites (Fig. 4), remains of *Arenaria serpyllifolia, Rumex acetosella*, *Origanum vulgare*, *Filipendula ulmaria*, *Cerastium holosteoides* and *Stellaria graminea* are most abundant. The samples differ in their qualitative and quantitative composition (ESM1). The results of PCA (Fig. 5) for grassland taxa separate Polanowo samples on the right side of the plot from Grodno samples scattered on the left side. The main factor separating samples from both sites is the presence of exclusive taxa. The large distances between samples from Grodno illustrate high taxonomic variability among individual samples from that site.

Wetland plants (Group 2) include 43 taxa (37 species), such as aquatics, plants growing in mires and in habitats periodically flooded. More taxa (34) were identified in Grodno than in Polanowo (22). Twelve taxa were found at both sites. Interestingly, despite the vessels' underwater positions, only a few taxa of typical aquatic plants were recorded, while rushes are represented by several taxa but with few specimens. The largest group of species found in large numbers (especially in Polanowo) comprises those from seasonally flooded lake banks, such as *Atriplex prostrata* s.l., *Ch. ficifolium*, *Ch. glaucum* and *Ch. rubrum.*

Group 3 includes plants associated with forests and forest edges, comprising 16 taxa (14 species) of trees, shrubs and forbs found in small numbers of remains. *Betula* sect. *albae* and *Fragaria vesca* are the most numerous.

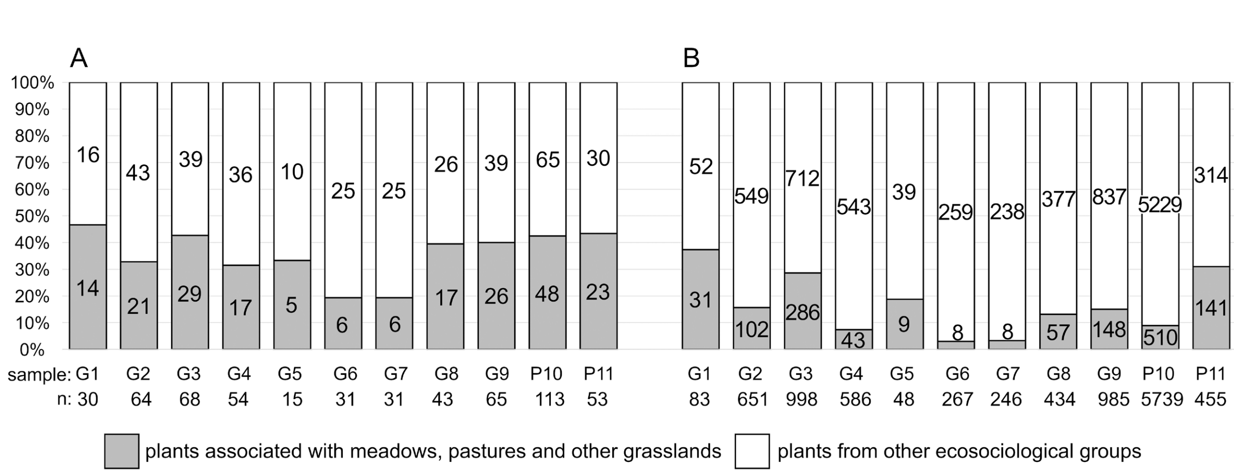

Figure 3. Percentage of taxa (**A**) and plant remains (**B**) associated with meadows, pastures, and other grasslands in relation to other ecosociological groups

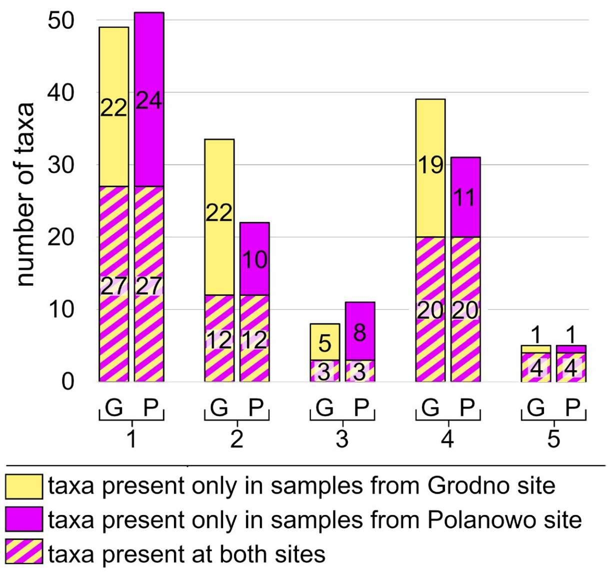

Figure 4. Number of taxa in each ecosociological group: 1 – plants associated with meadows, pastures, and other grasslands; 2 – wetland plants; 3 – plants associated with forests and forest edges; 4 – ruderal and segetal plants; 5 – cultivated plants

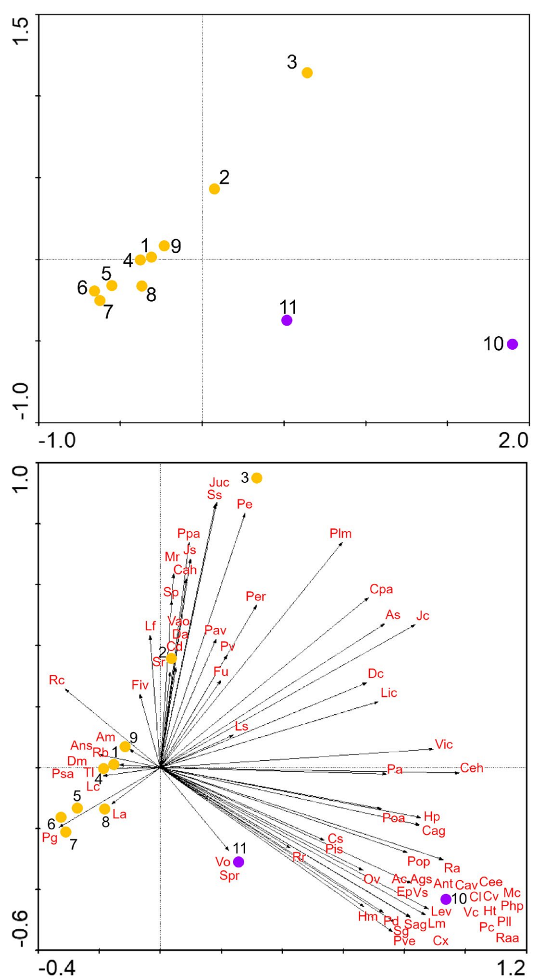

Figure 5. Principal component analysis (PCA) of samples from Grodno (yellow) and Polanowo (purple) in relation to the botanical composition of samples in the group of meadows, pastures, and other grasslands. Abbreviations for plants associated with meadows, pastures, and other grasslands are in the supplementary material (ESM2)

Ruderal and segetal weeds (Group 4) are the second best-represented vegetation type at both sites. This group includes 50 taxa (46 species) that grow in human-disturbed habitats or as crop weeds. Grodno contains 39 taxa (37 species), while Polanowo has 31 taxa (29 species). Twenty taxa are common to both sites. Remains of *Ch. album*, *Urtica dioica*, *Descurainia sophia*, *Solanum nigrum*, *Stellaria media* and *Fallopia convolvulus* are most frequent and abundant (ESM1). Forty-six seeds of *B. nigra* were found in sample G9 along with seeds of *Papaver somniferum*, glumes of *Panicum miliaceum* and many remains of wild species. This is one of the two earliest findings of this species in Poland and the most numerous in materials older than the High Medieval period (Lityńska-Zając, 2005). This record suggests that *B. nigra* may have been gathered and used as a condiment or medicinal plant by LUC farmers.

The list of cultivated plants (Group 5) includes cereals (*P. miliaceum*, *Triticum spelta* and Cerealia indet.) and oil/fiber plants (*Linum usitatissimum*, *P. somniferum* and *Camelina sativa*). Only in Polanowo remains of cultivated plants occur in large numbers (*P. miliaceum*, *P. somniferum* and *C. sativa*).

REPRESENTATION OF WETLAND AND OTHER GRASSLAND PLANT COMMUNITIES

Most grassland species identified in this study are characteristic of present-day semi-natural pastures, meadows and tall-herb meadow fringes developing on mesic and wet, fertile deep soils (*Molinio-Arrhenatheretea* class). The share of remains of these species relative to all grassland remains is 58% for Polanowo and 79% for Grodno. In Polanowo, they mostly occupied well-drained soils (*Arrhenatheretalia*: e.g. *Campanula patula*, *Cerastium holosteoides*, *Leucanthemum vulgare*, *Phleum pratense*, *Stellaria graminea*), whereas in Grodno, species indicative of wet, mineral and peaty soils (*Molinietalia caeruleae*: e.g. *Valeriana officinalis*, *Lythrum salicaria*, *Filipendula ulmaria*, *Lychnis flos-cuculi*) were dominant. Several species are typical of temporarily flooded or heavily grazed and trampled nutrient-rich meadows and pastures (*Potentillo-Polygonetalia avicularis*) such as *Plantago major*, *Juncus compressus*, *Ranunculus repens*, *Poa annua* and *Sagina procumbens*. This type of vegetation is much better represented in Grodno. Species typical of dry

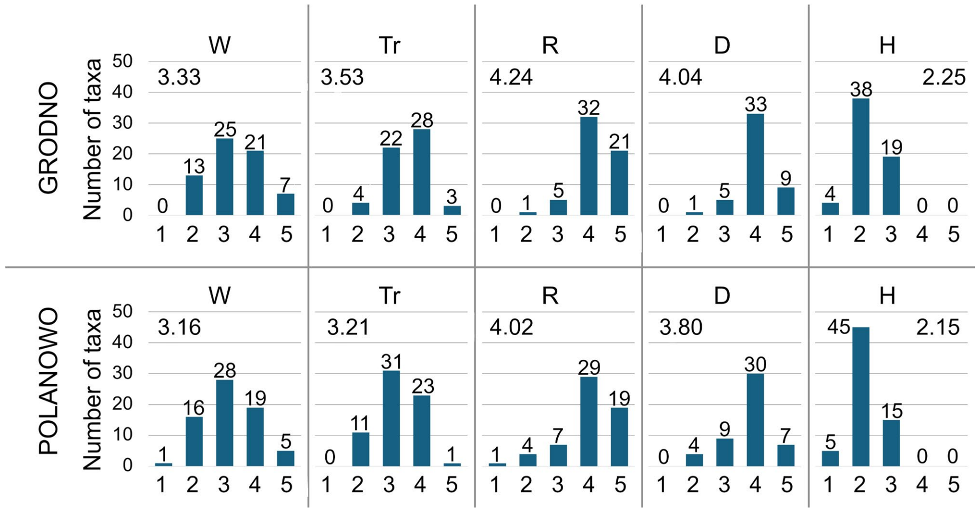

Figure 6. Indicator values (edaphic conditions) for species regarded as plants associated with meadows, pastures, and other grasslands. W – soil moisture value; Tr – trophy value; R – soil (water) acidity (pH) value; D – soil granulometric value; H – organic matter content value

grasslands developing on base- and colloid-rich soils (*Festuco-Brometea* class) form a distinct group at both sites (*Filipendula vulgaris*, *Campanula glomerata*, *Prunella grandiflora*, *Primula veris*, *Centaurea scabiosa* and *Ranunculus bulbosus*), but most species appear as single remains. In Polanowo, they constitute 10%, while in Grodno they make up 8%. The most numerous remains are those of *Origanum vulgare, Campanula glomerata* and *Primula veris*. Only a few species come from secondary dry swards developing on acid or neutral, nutrient-poor sandy soils, such as *Potentilla erecta*, *P. argentea*, *Rumex acetosella, Calluna vulgaris*, *Viola canina* and *Luzula multiflora*.

As mentioned above, the PCA plot (Fig. 5, Supplementary File 2[2]) reflects similarities and differences in the internal structure of samples based on the representation of grasslands in different habitats. It can be assumed that the number of grassland taxa in samples is one factor influencing this pattern. The most distant sample, P10, contains the highest number of grassland taxa, including 27 associated with the present-day *Molinio-Arrhenatheretea* class. A second factor may be that this sample includes taxa not found or less frequently recorded in other samples, and in P10, they occur in numerous remains. In the case of Grodno, most samples show a similar number and taxonomic composition of grassland plants. Sample G3 is a clear outlier, characterized by a significant accumulation of *Juncus* seeds, and other plants in this sample are also represented by a higher abundance of diaspores.

Wetland taxa also reflect different vegetation types (Table 2). At Polanowo, the lake's bank was overgrown with tall forb vegetation typical of seasonally flooded eutrophic habitats with *Chenopodium ficifolium*, *Ch. glaucum*, *Atriplex prostrata* s.l. and *Polygonum lapathifolium*. In Grodno, rushes with *Alisma plantago-aquatica*, *Schoenoplectus lacustris*, *Eleocharis palustris*/*uniglumis* and *Typha* sp. were better developed. At this site, remains of *Nuphar lutea*, *Nymphaea alba*, *Najas* sp., *Potamogeton* sp. and Characeae appear in low numbers, whereas in Polanowo, numerous oogonia of Characeae are present in the subfossil samples, consistent with the present-day aquatic vegetation dominated by stonewort meadows.

ECOLOGICAL INDICATORS OF THE EDAPHIC CONDITIONS

The ecological spectra of grassland species (excluding wetland taxa) reveal some differences between the sites, even though the average values for particular factors are rather similar (Fig. 6). At both sites, the distribution related to soil moisture values is similar, with the highest number of species preferring fresh soils and more taxa typical of moist soils than those of dry ones. The results indicate a slightly higher proportion of species from drier habitats in Polanowo. In both sites, the distribution of species according to trophy values shows dominance of those growing on mesotrophic and

[2] Supplementary File 2: Abbreviations for plant taxa associated with meadows, pastures and other grasslands used in the PCA

Table 2. List of plant taxa associated with meadows, pastures, other grasslands and wetlands. I – total number of plant remains in all samples at a site; II – number of samples in which the taxon was present; III – percentage of remains within each group

Site	GRODNO (n = 9)			POLANOWO (n = 2)		
	I	II	III (%)	I	II	III (%)
PLANTS ASSOCIATED WITH MEADOWS, PASTURES AND OTHER GRASSLANDS						
Wet grasslands						
Agrostis stolonifera L.	–	–	–	2	1	1.31
Carex cfr. *distans* L.	2	1	0.65	–	–	–
Carex ovalis Gooden.	–	–	–	1	1	0.65
Carex panicea L.	–	–	–	1	1	0.65
Carex cfr. *panicea* L.	3	1	0.97	–	–	–
Deschampsia cespitosa (L.) P. Beauv.	1	1	0.32	–	–	–
cfr. *Deschampsia cespitosa* (L.) P. Beauv.	1	1	0.32	–	–	–
Epilobium palustre L.	–	–	–	3	1	1.96
Filipendula ulmaria (L.) Maxim.	28	7	9.03	4	1	2.61
Hypericum tetrapterum Fr.	–	–	–	2	1	1.31
Juncus conglomeratus L. / *effusus* L.	163	4	52.58	106	2	69.28
Juncus subnodulosus Schrank	15	3	4.84	–	–	–
Lychnis flos-cuculi L.	9	5	2.90	1	1	0.65
Lythrum salicaria L.	16	2	5.16	2	2	1.31
Molinia caerulea (L.) Moench	–	–	–	2	1	1.31
Poa palustris L.	6	1	1.94	19	2	12.42
Puccinellia distans (Jacq.) Parl.	–	–	–	5	2	3.27
Ranunculus repens L.	4	3	1.29	3	1	1.96
Rumex crispus L.	5	5	1.61	–	–	–
Scirpus sylvaticus L.	4	3	1.29	–	–	–
Stellaria palustris Retz.	8	3	2.58	–	–	–
Thalictrum lucidum L.	2	1	0.65	–	–	–
Valeriana officinalis L.	43	6	13.87	2	1	1.31
Sum of remains	310			153		
Number of species	14			13		
% of meadow species	30.43			26.00		
Mesic and semi-dry grasslands						
Achillea millefolium L.	1	1	1.47	–	–	–
Anthriscus sylvestris (L.) Hoffm.	2	2	2.94	–	–	–
Campanula patula L.	–	–	–	47	2	21.86
Centaurium erythraea Rafn	–	–	–	2	1	0.93
Cerastium holosteoides Fr. emend. Hyl.	29	7	42.65	78	2	36.28
Dactylis glomerata L.	3	1	4.41	–	–	–
Daucus carota L.	3	2	4.41	2	2	0.93
Hypericum maculatum Crantz	–	–	–	37	2	17.21
Leontodon autumnalis L.	2	1	2.94	–	–	–
Leucanthemum vulgare Lam.	–	–	–	9	2	4.19
Melandrium rubrum (Weigel) Garcke	4	3	5.88	–	–	–
Pastinaca sativa L.	2	1	2.94	–	–	–
Phleum pratense L.	–	–	–	5	1	2.33
Plantago lanceolata L.	–	–	–	1	1	0.47
Primula cfr. *elatior* (L.) Hill	1	1	1.47	–	–	–
Prunella vulgaris Huds.	14	4	20.59	1	1	0.47
Ranunculus acris L.	–	–	–	1	1	0.47
Stellaria graminea L.	7	4	10.29	29	2	13.49
Veronica chamaedrys L.	–	–	–	3	1	1.40
Sum of remains	68			215		
Number of species	11			12		
% of meadow species	23.91			24.00		
Trampled grasslands						
Carex hirta L.	6	2	3.68	–	–	–
Juncus compressus Jacq.	26	3	15.95	–	–	–
Plantago major L.	35	5	21.47	7	1	29.17
Poa annua L.	3	1	1.84	6	1	25.00
Polygonum aviculare L.	93	9	57.06	10	2	41.67
Sagina procumbens L.	–	–	–	1	1	4.17
Sum of remains	163			24		
Number of species	5			4		
% of meadow species	10.87			8.00		

Table 2. Continued

Site	GRODNO (n = 9)			POLANOWO (n = 2)		
	I	II	III (%)	I	II	III (%)
Basiphilous dry grasslands and steppe grasslands						
Anthemis tinctoria L.	–	–	–	1	1	0.99
Arenaria serpyllifolia L.	32	5	35.96	23	2	22.77
cfr. *Arenaria serpyllifolia* L.	9	1	10.11	–	–	–
Artemisia campestris L.	–	–	–	1	1	0.99
Campanula glomerata L.	4	3	4.49	12	2	11.88
Centaurea scabiosa L.	1	1	1.12	1	1	0.99
Clinopodium vulgare L.	–	–	–	3	1	2.97
Filipendula cfr. *vulgaris* Moench	2	1	2.25	–	–	–
Filipendula vulgaris Moench	1	1	1.12	–	–	–
Hypericum perforatum L.	2	2	2.25	6	2	5.94
Linum catharticum L.	19	5	21.35	10	2	9.90
Origanum vulgare L.	12	5	13.48	15	2	14.85
Pimpinella saxifraga L.	1	1	1.12	1	1	0.99
Poa compressa L.	–	–	–	6	1	5.94
Primula veris L.	2	1	2.25	16	2	15.84
cfr. *Prunella grandiflora* (L.) Scholler	1	1	1.12	–	–	–
Prunella grandiflora (L.) Scholler	1	1	1.12	–	–	–
Ranunculus bulbosus L.	1	1	1.12	–	–	–
Saxifraga cfr. *granulata* L.	–	–	–	5	2	4.95
Stachys recta L.	1	1	1.12	–	–	–
Veronica spicata L.	–	–	–	1	1	0.99
Sum of remains	89			101		
Number of species	12			14		
% of meadow species	26.09			28.00		
Dry swards on poor sandy soil						
Potentilla argentea L. s.str.	7	3	13.21	11	1	6.96
Rumex acetosella L.	16	5	30.19	120	2	75.95
Calluna vulgaris (L.) Hull	–	–	–	3	1	1.90
Luzula campestris (L.) DC. / *multiflora* (Retz.) Lej.	8	2	15.09	–	–	–
Luzula multiflora (Retz.) Lej.	–	–	–	14	2	8.86
Potentilla erecta (L.) Raeusch.	20	5	37.74	2	1	1.27
Veronica officinalis L.	–	–	–	1	1	0.63
cfr. *Viola canina* L.	2	1	3.77	–	–	–
Viola canina L.	–	–	–	7	1	4.43
Sum of remains	53			158		
Number of species	4			7		
% of meadow species	8.70			14.00		
Total sum of remains	683			651		
Total number of species	46			50		
WETLAND PLANTS						
Seasonally flooded alluvia and lacustrine banks						
Althaea officinalis L.	–	–	–	1	1	0.10
Atriplex prostrata s.l. Boucher ex DC.	–	–	–	310	2	30.48
Chenopodium ficifolium Sm.	30	4	11.63	307	2	30.19
Chenopodium glaucum L.	–	–	–	30	1	2.95
Chenopodium glaucum L. / *rubrum* L.	3	1	1.16	–	–	–
Chenopodium cfr. *rubrum* L.	1	1	0.39	–	–	–
Chenopodium rubrum L.	–	–	–	20	1	1.97
Polygonum hydropiper L.	1	1	0.39	–	–	–
Polygonum cfr. *lapathifolium* L.	1	1	0.39	–	–	–
Polygonum lapathifolium L.	174	8	67.44	335	2	32.94
Polygonum cfr. *mite* Schrank	2	1	0.78	–	–	–
Ranunculus sceleratus L.	23	6	8.91	5	2	0.49
Rumex cfr. *maritimus* L.	3	1	1.16	–	–	–
Rumex maritimus L.	1	1	0.39	–	–	–
Rumex cfr. *palustris* Sm.	3	1	1.16	–	–	–
Myosoton aquaticum (L.) Moench	11	3	4.26	8	2	0.79
Calamagrostis pseudophragmites (Haller fil.) Koeler	3	1	1.16	–	–	–
Eupatorium cannabinum L.	2	1	0.78	1	1	0.10
Sum of remains	258			1017		
Number of species	11			9		
% of wetlands species	39.29			0.45		

Table 2. Continued

Site	GRODNO (n = 9)			POLANOWO (n = 2)		
	I	II	III (%)	I	II	III (%)
Reed and tall sedge swamps						
Alisma plantago-aquatica L.	90	7	52.63	–	–	–
Carex cfr. *elata* All.	1	1	0.58	–	–	–
Carex paniculata L.	–	–	–	1	1	3.13
Eleocharis palustris (L.) Roem. et Schult.	–	–	–	1	1	3.13
Eleocharis palustris (L.) Roem. et Schult./ *uniglumis* (Link) Schult.	9	4	5.26	–	–	–
Epilobium hirsutum L.	2	1	1.17	21	1	65.63
Lycopus europaeus L.	13	5	7.60	–	–	–
Mentha aquatica L.	9	3	5.26	1	1	3.13
Phalaris arundinacea L.	3	1	1.75	–	–	–
Phragmites australis (Cav.) Trin. ex Steud.	–	–	–	8	2	25
Schoenoplectus lacustris (L.) Palla	12	5	7.02	–	–	–
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	2	1	1.17	–	–	–
Schoenoplectus lacustris (L.) Palla / *tabernaemontani* (C.C . Gmel.) Palla	15	4	8.77	–	–	–
Typha sp.	15	5	8.77	–	–	–
Sum of remains	171			32		
Number of species	8			5		
% of wetlands species	28.57			0.25		
Fens and transitional mires						
Galium palustre L.	5	2	3.73	–	–	–
Juncus articulatus L. emend. K. Richt.	118	4	88.05	32	2	100
Menyanthes trifoliata L.	8	3	5.97	–	–	–
cfr. *Menyanthes trifoliata* L.	2	2	1.49	–	–	–
Ranunculus flammula L.	1	1	0.74	–	–	–
Sum of remains	134			32		
Number of species	4			1		
% of wetlands species	0.14			0.05		
Ephemeral vegetation on periodically flooded habitats						
Gypsophila muralis L.	–	–	–	2	1	8.33
Juncus bufonius L.	60	3	92.31	15	2	62.50
Potentilla norvegica L.	5	3	7.69	5	1	20.83
Stellaria uliginosa Murray	–	–	–	2	1	8.33
Sum of remains	65			24		
Number of species	2			4		
% of wetlands species	7.14			0.20		
Aquatic plants						
Characeae	13	2	39.39	295	2	99.33
Lemna sp.	–	–	–	1	1	0.34
Najas marina L.	–	–	–	1	1	0.34
Najas sp.	2	1	6.06	–	–	–
Nuphar lutea (L.) Sibth. et Sm.	6	2	18.18	–	–	–
Nymphaea alba L.	1	1	3.03	–	–	–
Potamogeton cfr. *natans* L.	1	1	3.03	–	–	–
Potamogeton sp.	10	2	30.30	–	–	–
Sum of remains	33			297		
Number of species	3			1		
% of wetlands species	10.71			0.05		
Total sum of remains	661			1402		
Total number of species	28			20		

eutrophic soils, but at Grodno species from eutrophic habitats prevail over those from mesotrophic ones, while the opposite trend is shown by the data from Polanowo. Poor, oligotrophic habitats are distinctly better represented at Polanowo. Although data from both sites indicate the dominance of taxa preferring neutral soils and a notable share of those favoring alkaline soils, the results from Polanowo illustrate more diversified soil reaction parameters, including the presence of acid soils. The data from both sites show similar spectra concerning physical soil structure (granulometric indices) and organic matter content, indicating the dominance of mineral-humic soils developed on sandy-clayey or clayey-sandy substrates as habitats for grasslands. In summary, these data suggest more diversified habitat conditions and the presence of patches of nutrient-poor soils around the Polanowo site.

DISCUSSION

THE ORIGIN OF PLANT REMAINS IN THE VESSELS

The origin of the plant remains preserved in the study vessels and the archaeological contexts of these findings are important aspects for interpreting the archaeobotanical data. As mentioned earlier, these vessels might have been placed as foundation offerings at a palisade and a bridge (Grodno) and at two building constructions (Polanowo) (Gackowski, 2010; Pydyn and Rembisz, 2010). However, it remains uncertain whether the plant materials found in the vessels originate, at least partly, from an intentional deposition of plants collected for the ceremony or whether the vessels were left empty and later gradually filled with local plant material until they have been covered with lake sediments.

The botanical composition of the vessel contents from both sites is complex, and the large number of species from different plant communities, including some crops, does not provide unambiguous evidence to answer this question. However, some hints to test both hypotheses come from the taxonomic peculiarities of the datasets.

Hypothesis I: The originally empty vessels gradually filled with plant material from local vegetation and various activities on the sites. The main argument for this hypothesis is the prevalence of ruderal plants, field weeds, and species typical of wet habitats, which were certainly widespread around the settlements and in their immediate surroundings. The heterogeneity of species composition and the presence of useful plants may reflect various uses of plant material in the settlements, such as animal fodder, construction materials and elements of human diet.

Hypothesis II: The botanical content of the vessels is, at least in part, the result of deliberate deposition of plant material.

In general, the comparison of datasets from both sites shows great similarities. Characteristic features include large proportions of species common to both sites, similar proportions of taxa representing particular vegetation groups (except cultivated plants), and mass occurrences of seeds and fruits of Chenopodiaceae and Polygonaceae in the study samples. Moreover, the plant macrofossil spectra from the vessels in Grodno and, to a great extent, in Polanowo, are typical for cultural layers formed in archaeological wetland sites, which usually contain a large representation of local wetland and ruderal vegetation with an admixture of remains of plants transported to settlements for various uses (Behre, 1976; Latałowa, 1999; Pińska and Latałowa, 2014; Badura et al., 2018; Maciejewska et al., 2022). Therefore, Hypothesis I seems the most likely explanation for the Grodno results, while interpretations for Polanowo are more complex.

The results from Polanowo suggest at least three sources of the plant remains accumulated in the vessels. Similar to Grodno, a part of the remains represents local vegetation and plant material dispersed over the settlement due to human activity. A distinct admixture of aquatic taxa is certainly caused by flooding of the site and reflects the underwater position in which the vessels were found. Finally, following the arguments for Hypothesis II, intentional deposition of some plant material could be considered a third potential source of the remains. At least three facts support this hypothesis. 1 – In both vessels from Polanowo, remains of cultivated plants occur in large numbers, including numerous seeds of *Camelina sativa* and *Papaver somniferum*, which in cultural layers not associated with specific archaeological objects, such as vessels, kitchen vast or latrines, are usually highly dispersed. 2 – In these vessels, seeds of *Chenopodium album* and other species of Chenopodiaceae and Polygonaceae constitute approximately 73 and 30% of the samples. It should be emphasized that due to the "conservation" of the vessel contents by lake sediments, contamination of the original fillings by recent diaspores can be excluded – a frequent problem in archaeobotanical materials where fossil and recent seeds of *C. album* occur together and are difficult to separate (Mueller-Bieniek et al., 2018). Therefore, the high concentration of seeds of these taxa may suggest they were collected and deliberately placed in the vessels. Many earlier studies have shown these plants have been gathered and used as food from prehistoric times until recent times (Kluk, 1805; Helbaek, 1959; Knörzer, 1967; Bogaard, 2004; Łuczaj and Szymański, 2007; Behre, 2008; Kofel et al., 2017; Nielsen et al., 2021). Interestingly, Mueller-Bieniek et al. (2018, 2019) provided several arguments for the potential cultivation of *Ch. album* in the Early Neolithic in Kuyavia, the region neighboring both study areas. Stokes and Rowley-Conwy (2002) also demonstrated through experiments that *Ch. album* can serve as an alternative to cereals due to its broadly comparable return rates, suggesting possible cultivation in the Iron Age. In the context of the potential ritual role of the vessels from Polanowo, the suggestion by Hald et al. (2024), that the findings of *Ch. album* and *Polygonum lapathifolium* as main ingredients of the last meals of sacrificed men (bog bodies) from the Iron Age in Denmark may indicate that mixing of crops and wild taxa could also have a ritual character, is especially interesting. 3 – Both vessels from Polanowo also contained remains of species originating from different habitats and known for long tradition of their medicinal or magical uses (e.g. *Fragaria vesca*, *Primula veris*, *Saxifraga tridactylites* or *S. granulata*, *Origanum vulgare*, *Linum catharticum*, *Leucanthemum vulgare*, *Hypericum maculatum*, *H. perforatum*, *Clinopodium vulgare*, *Centaurium erythraea*, *Campanula patula* and *C. glomerata*) (Kluk, 1805, 1808, 1811; Kujawska et al., 2016).

The archaeological arguments for a possible role of the vessels from Polanowo and Grodno as foundation offerings (Gackowski, 2010; Pydyn and Rembisz, 2010) align well with many findings from various periods, cultural units and geographic locations. These suggest similar rituals aimed at magical protection of private buildings, sanctuaries, or other constructions, such as wells, ramparts, gates, or bridges (Hilczer-Kurnatowska, 1982; McCarty et al., 2019). Most foundation offerings consist of animal bones and pottery, although other types of artifacts have also been used for this purpose (Lepówna, 1981; Dalewski, 1990; Paulsson-Holmberg, 1998; Rovira and Chabal, 2008; Baron, 2012; Heske et al., 2012; Nießen, 2017; Kajkowski, 2022). Unfortunately, unlike other kinds of offerings, published reports on plant material found in potential foundation deposits remain relatively scarce. Notable exceptions include findings from Pompeii (Robinson, 1999, 2002; Ciaraldi and Richardson, 2000) and the Roman port of Lattara (Rovira and Chabal, 2008), where carbonized cereals, pulses, flax seeds and various fruit remains formed part of these features. Ceramic vessels presumed to be foundation offerings have been discovered at several LUC and Early Medieval sites in Poland; however, only a few have had their plant remains analysed. In this regard, the botanical content of two vessels from the Early Medieval site of Żółte (an island on Lake Zarańskie, northwestern Poland) is of particular interest, because the subfossil assemblages show similarities to those from Polanowo (Pińska and Latałowa, 2014). There is also evidence of foundation deposits containing Early Medieval pottery with cereal remains from Żlinice (Hilczer-Kurnatowska, 1982) and Ostrów Lednicki (Polcyn, 1995), as well as a porridge-like deposit from Bonikowo (Klichowska, 1964) and Żmijowiska (analysed by G. Skrzyński; PAP – Science and Scholarship in Poland 201). At the latter site, a vessel contained a mixture of fruits and seeds from wild and cultivated plants, including large quantities of *Chenopodium album* along with *Atriplex* sp., *Polygonum* sp., *Rumex* sp., *Mentha arvensis*, *Hordeum vulgare*, *Panicum miliaceum*, *Triticum spelta* and *Lens culinaris*. In summary, although the nature of the subfossil material from Polanowo does not allow an unequivocal statement about its ritual origin, the Hypothesis II may be considered and should encourage more careful analysis of botanical contents in similar objects. This practice is still not common, not only in Polish archaeological research (Lodwick, 2015).

SOME HINTS FOR THE DISCUSSION ON THE HISTORY OF GRASSLANDS IN NORTH-CENTRAL EUROPE

Similar to pollen data from most regions of Poland (Ralska-Jasiewiczowa et al., 2004), numerous records from Wielkopolska – including the Gniezno Lakeland (Tobolski, 1990; Filbrandt-Czaja, 1998; Milecka, 1998; Niewiarowski and Noryśkiewicz, 1999; Makohonienko, 2000) and the Chełmno Lakeland (Filbrandt-Czaja, 2009; Noryśkiewicz, 2013), dated to the Late Bronze and Early Iron Ages, indicate a growing extent of open land at the expense of woodland and finally strong limitation of broad-leaved forests with elm, lime, oak and hornbeam, alongside alder woods prevailing in wetlands. The presence of cereal pollen types, a high proportion of grasses, and a broad spectrum of forb pollen suggest the important role of farming and large-scale landscape transformation during the rising LUC occupation. Increasing proportions and diversity of pollen types usually regarded as indicators of various grassland communities – such as *Plantago lanceolata*, *Rumex acetosa*-type, *Filipendula*, Poaceae, *P. media*, *Ranunculus acris*-type, *Arenaria*-type, *Trifolium pratense*-type, *Centaurea jacea*-type, Asteraceae and many others, illustrate the development of pastures and, likely, meadows.

In general, the interpretation of archaeobotanical data for reconstructing ancient plant communities faces a number of constraints. These arise not only from the fragmentary nature and complex origins of the materials but also from various natural and anthropogenic factors that have transformed plant communities over thousands of years (Behre and Jacomet, 1991; Lityńska-Zając and Wasylikowa, 2005). This also applies to the materials analysed in this study, which represent thanatocoenoses *sensu* Willerding (1991), meaning that their botanical content originates from multiple sources. The large number of species with differing habitat requirements indicates that diversified landscapes with a significant share of open land surrounded both sites.

The origin and history of particular grassland types differ among geographic and cultural regions and specific habitats (Bush, 1993; Poschlod et al., 2009; Hejcman et al., 2013; Feurdean et al., 2018; Robin et al., 2018). According to palaeoecological data, in north-central Europe, patches of wet grasslands have persisted throughout the entire Holocene within wetlands in river valleys and lake channels. The mass spread of *Filipendula ulmaria* at the very beginning of the Holocene and its high presence in wetland vegetation until the establishment of alder woods in the mid-Holocene is well-documented in many pollen diagrams (Miotk-Szpiganowicz et al., 2004) and confirmed by macrofossil data (e.g. Latałowa et al., 2013; Gołaszewska et al., 2019). Moreover, numerous subfossil seeds of *Epipactis palustris* and *Dactylorhiza incarnata*/*maculata* complex found in sediments of the Wieprza River floodplain (northern Poland) suggest high floristic diversity in these grasslands as early as the early Holocene (Gołaszewska et al., 2019). Although the mid-Holocene expansion of riverine-type forests and the gradual overgrowth of some marshes by water-tolerant trees and shrubs, such as black alder and willows led to a decrease in wetland openness, grassland species continued to find suitable conditions within a mosaic of wetland habitats. Some macrofossil records even indicate the persistence of open mires, hosting numerous species frequent in wet grasslands, throughout the entire Holocene (Latałowa, 1982; Latałowa et al., 2013; Pędziszewska and Latałowa, 2016). Since the Neolithic, during successive periods and settlement phases, wetlands in river valleys and lake channels were a source of raw wood, animal fodder and litter. The exploitation of alder woods by LUC farmers is confirmed by a distinct decline of the *Alnus* pollen in the diagram from Lake Grodzieńskie (Filbrandt-Czaja, 2009) and many other regional pollen records. Archaeological data also indicate the use of alder timber for construction in LUC settlements (Gackowski, 2003; Ważny, 2010). Various plants commonly found at wetland archaeological sites (e.g. *Phragmites australis*, *Juncus* spp., *Carex* spp.), were undoubtedly collected for multiple purposes. For instance, Fitzke (1938/1939) suggested that the roofs of the Biskupin stronghold were likely thatched with *Phragmites*. During periods of low availability of forest foods (mast, mushrooms), wetlands may also have been used for pig breeding, which was an important part of livestock (Poschlod et al., 2009). Multidirectional uses of wetlands influenced species competition through changes in light availability, habitat fertility, and local hydrology, enabling population expansions of several previously minor plants, especially small forbs. Present-day observations in wetlands (Kulik et al., 2023) support the idea that these processes led to the ecological transformation of some wetland patches into wet grasslands. It appears that such changes were already well underway in areas occupied by LUC settlements, as evidenced by the large number of wet grassland species in archaeobotanical materials from sites associated with this culture in Poland (Jaroń, 1938; this study). On temporarily flooded and heavily grazed sites, nutrient-rich vegetation typical of wet grassland communities of the *Potentillo-Polygonetalia avicularis* was spreading. Moreover, several species diagnostic of these grasslands also occur in other human-impacted habitats such as trampled grassland paths, tracks, or cultivated fields enriched by nitrogen compounds (Mucina et al., 2016; Kącki et al., 2020), further confirming the distinct impact of human activity around both sites.

In the study regions, the history of grassland types developing on dry grounds is closely linked to the gradual thinning of forests. Some light-demanding and temperature-tolerant species, already present in the late-glacial flora, survived in forest gaps and at forest edges bordering river valleys, lakes and mires, as evidenced by pollen diagrams showing the continuous presence of several herb pollen types throughout the Holocene. Other species spread with climate warming through migration facilitated by birds and herbivores (zoochory), as well as dispersal by wind (anemochory) and along watercourses (hydrochory). Natural and anthropogenic fires (Dietze et al., 2018) and large herbivore grazing (Vera, 2000) created favorable conditions for light-demanding grasses and forbs, both during the early Holocene when forests – mainly pine, birch and later hazel – had a relatively open structure, and in the mid-Holocene when northern Central Europe was dominated by dense broad-leaved forests (Nielsen et al., 2012; Zanon et al., 2018). High frequencies of *Pteridium aquilinum* spores in many pollen profiles from northern and central Poland confirm the presence of forest glades where heliophilous plants could found favourable conditions for their growth and proliferation long before the spread of agriculture (Latałowa, 1992; Makohonienko, 2000). Since the Neolithic, periods of settlement activity brought increased demand for timber and firewood, along with burning, livestock grazing in forests and coppicing (Dufraisse, 2008; Kłusek and Kneisel, 2021), all of which contributed to forest thinning and the spread of grassland species such as *Plantago lanceolata*, *Rumex acetosa*, *R. acetosella*, *C. vulgaris* and others, as indicated in many of the previously mentioned regional pollen diagrams. Palynological evidence of these processes, including traces of fires, is particularly distinct in the sections of pollen profiles corresponding to the late LUC settlement phase. Archaeobotanical data from Poland indicate a rising trend in species diversity within these grassland types from the Neolithic to the Early Iron Age (Lityńska-Zając, 2005), consistent with findings from Germany (Knörzer, 1996), the Czech Republic (Pokorná et al., 2018) and Britain (Greig, 1988). Taken together with results from the present study, it can be inferred that LUC societies exploited a full range of forest habitats around their settlements, leading to the development of pasture and meadow patches representing early successional stages of various grassland communities.

The high representation of species typical of present-day semi-natural vegetation classified as *Molinio-Arrhenatheretea* suggests the presence of extensively used wet and mesic grasslands on fertile, deep soils around both sites during the LUC period. This type of vegetation comprising a broad spectrum of grassland communities is highly variable, biodiverse, and sensitive to environmental changes (Roo-Zielińska, 2001; Mucina et al., 2016; Kącki et al., 2020). Moisture availability and the intensity of grazing and mowing are key factors influencing their formation and dynamics, including transitions between different grassland communities (Chabuz et al., 2019). In the Early Iron Age, patches of vegetation corresponding to present-day *Molinietalia caeruleae* developed on wet, mineral-humic soils around the settlements at Grodno and Polanowo. The presence of species diagnostic of fen communities (*Scheuchzerio-Caricetea fuscae* class), alder forests (*Alnetea glutinosae* class) and riparian forests (*Fraxino-Alnetum*) provides insight into the origins of these grasslands, which likely developed as secondary vegetation under increasing economic exploitation (Matuszkiewicz, 2001). Several species diagnostic for wet grasslands – such as *Thalictrum lucidum*, *Filipendula ulmaria*, *Lycopus europaeus*, *Lychnis flos-cuculi* and *Polygonum bistorta* – recovered at Biskupin (Jaroń, 1938) confirm that this type of vegetation was commonly exploited economically in areas surrounding LUC settlements in the study region, where such habitats were widespread.

The occurrence of a rather large group of species diagnostic for present-day mesic or even sub-xeric meadows and pastures on more fertile soils (order *Arrhenatheretalia elatioris*) may reflect the initial phase of such grassland development. Today, grazing and mowing are important for maintaining their high biodiversity by improving light conditions for many short forbs (Klimešová et al., 2008). These grasslands are considered among the most characteristic secondary plant communities, mainly developing after oak-hornbeam forests (*Carpinion*) and the driest forms of riverine forests (*Ficario-Ulmetum*) (Matuszkiewicz, 2001). Pollen data from both regions

(Makohonienko, 2000; Noryśkiewicz, 2013) and local data from Lake Grodno (Filbrandt-Czaja, 2009) and Biskupin (Niewiarowski and Noryśkiewicz, 1999) confirm this, showing strong declines in *Carpinus* and *Quercus* and other deciduous trees, alongside increasing proportions and richness of non-arboreal pollen in sections of the pollen profiles dated to the Late Bronze and Early Iron Ages.

Interestingly, several of our records, as well as those from Biskupin, revealed species diagnostic for steppic semi-dry grasslands developing on neutral or basic soils, currently classified as *Festuco-Brometea* (Matuszkiewicz, 2001; Willner et al., 2019). According to Willner et al. (2019), in Poland, patches of such grasslands represent extrazonal plant communities from two alliances within the order *Brachypodietalia pinnati*: *Cirsio-Brachypodion pinnati* and, less frequently, *Armerion elongatae*. They are mainly distributed on loess uplands in southern Poland, but more isolated stands also occur in northern parts of the country, including the study regions (Ceynowa, 1968; Filipek, 1974; Prajs et al., 2010; Kajtoch et al., 2016). For many decades, the historical biogeography of steppic grasslands in Central Europe has been debated (Kozłowska, 1931; Gradmann, 1933; Ložek, 1973), but recent studies supplied the new palaeobotanical (Bieniek, 2002; Kohler-Schneider and Caneppele, 2009; Magyari et al., 2010; Moskal-del Hoyo et al., 2017, 2025), palaeozoological (Németh et al., 2017; Horáčková et al., 2023), phylogeographical (Paul, 2012; Kajtoch et al., 2016; Willner et al., 2021) and multiproxy (Kuneš et al., 2015; Pokorný et al., 2015; Feurdean et al., 2018; Moskal-del Hoyo et al., 2018) studies have shed more light on the origin and history of this vegetation type in Central Europe. The main conclusions from these studies, summarized in a review by Feurdean et al. (2018), indicate that some important primary and secondary refugia for steppe species in Central Europe were located in the lower mountain ranges around the Pannonian Basin, where patches of Late Pleistocene hemiboreal-type open-canopy forest (a kind of forest-steppe) could harbor several species of semi-dry grasslands. There is also growing evidence for the local persistence of such vegetation throughout the Holocene due to the openness of forests in this region, with further spread driven by human activity. Recent palaeoecological and archaeobotanical studies in loess uplands in southern Poland suggest a similar scenario (Moskal-del Hoyo et al., 2017, 2018; Moskal-del Hoyo, 2021). Based on a large anthracological dataset, the authors hypothesize that already prior to the early Neolithic occupation in the mid-Holocene, the loess-mantled regions were mostly covered by open canopy oak and oak-pine forests similar to present-day subcontinental dry-mesic oak forests (*Potentillo albae-Quercetum*), which could harbor heliophilous plants typical of xerothermic grasslands. Moreover, phylogeographical data imply that these areas, lying south of the extent of the ice sheets during most Pleistocene glaciations, could serve as additional refugia for eurythermic steppe species (Kajtoch et al., 2016). In fact, the oldest late-glacial pollen sections from the Kraków-Częstochowa Upland reveal a well-developed steppe vegetation with taxa such as *Artemisia* spp., *Helianthemum* spp., *Bupleurum* sp., *Sanguisorba minor*, *Armeria* sp. and others (Latałowa, 1976; Latałowa and Nalepka, 1987). Possibly, a portion of these light-demanding, xerophilous and eurythermic species persisted under the semi-open canopy of early Holocene pine-birch forests as well as in the herb layer of the following forest communities, distinguished by high proportions of pine and hazel (Latałowa and Nalepka, 1987), and then in patches of mid-Holocene open-canopy oak and oak-pine forests described by Moskal-del Hoyo (2021).

The history of steppic grasslands in northern and north-central Poland, areas covered by the ice sheet during all Pleistocene glacial periods, is different. Some species typical of the so-called "cold steppe," such as *Artemisia* spp., *Helianthemum* spp., *Rumex acetosella*, *Gypsophila fastigiata*, *Sanguisorba minor* and *S. officinalis*, immigrated here after the retreat of the ice sheet during the Late Glacial period of the last glaciation (Vistulian/Weichselian Glaciation), as evidenced by the palaeoecological records (Ralska-Jasiewiczowa et al., 1998; Latałowa, 1999). In the Holocene, the development of forest cover resulted in fragmentation and strong restriction or disappearance of open habitats; nevertheless, some isolated populations of light-demanding, xerophilous plants could persist in forest openings and at forest edges up to the mid-Holocene. The mid-Holocene forest cover was also not an absolute barrier for the migration of some thermophilous species currently classified as typical for *Festuco-Brometea*, such as *Anthericum* spp., whose pollen has been recorded in several sediment samples from Lake Gościąż (central Poland) (Ralska-Jasiewiczowa et al., 1998; Ralska-Jasiewiczowa and Van Geel, 1998). However, we may suspect that the formation of steppic grassland communities in the study area began with increasing forest disturbances in the Neolithic. High frequencies of charred remains of *Stipa pennata* and occurrences of pollen of *Anthericum* and *Jasione* in materials from Early Neolithic sites in Kuyavia (a region bordering both the Gniezno and Chełmno Lakelands) strongly suggest the presence of xeric grassland patches in this area (Bieniek, 2002; Mueller-Bieniek and Nalepka, 2010). Increasing land opening caused by LUC settlements certainly fostered the development of such vegetation in suitable habitats in the study regions, where patches of *Festuco-Brometea* plant communities still exist (Ceynowa, 1968; Brzeg and Wojterska, 2001). In this context, the presence of relatively large fragments of the thermophilous oak forest *Potentillo albae-Quercetum* described in the current botanical survey near Polanowo (Kwiatkowska and Wyszomirski, 1988) may confirm the occurrence of potential habitats for semi-dry steppic grasslands, which could develop after cattle grazing in such woods (Moskal-del Hoyo, 2021).

Our data also suggest that vegetation typical of dry swards developing on acidic sandy soil occurred around the study sites. Although the list of taxa is rather short, the number of remains of *Rumex acetosella*, *Potentilla erecta* and *Potentilla argentea* indicates that their presence in the materials from both sites is not accidental. Moreover, rising frequencies of *Calluna* in pollen diagrams from both regions point to increasing openness in poor habitats (Makohonienko, 2000; Filbrandt-Czaja, 2009). This kind of grassland is secondary vegetation formed after intensive grazing by sheep and cattle in forests on poor soils (Matuszkiewicz, 2001).

Interestingly, although our material is limited to a few vessel fillings, the results reflect ecological differences between sites consistent with present-day environmental data. The list of taxa and the distribution of ecological indices of edaphic factors for Polanowo suggest more diversified habitat conditions and the presence of less fertile soils around this site than around Grodno, which aligns with maps of natural potential vegetation for these sites. This seems to confirm earlier findings that an adequately large macrofossil dataset containing species from various habitats may properly reflect environmental conditions around study sites (Latałowa et al., 2003).

POTENTIALS AND LIMITATIONS IN RECONSTRUCTING THE HISTORY OF GRASSLAND MANAGEMENT

Our interpretation of the data from Polanowo and Grodno sheds light on the development of grassland communities in the study regions, but also clearly reflects the limitations of archaeobotanical materials for reconstructing potential vegetation and its management in prehistoric landscapes. The latter issue, which is closely related to the question of the beginnings of haymaking, appears to be the most problematic (Greig, 1983; Hodgson et al., 1999; Hejcman et al., 2013; Poschlod, 2015). Definitive identification of hay in archaeological contexts is rare and usually concerns features dated to the Roman Iron Age and later periods, for which there is broad consensus that mown meadows were already part of the economy across much of Europe (Behre and Jacomet, 1991; Van Zeist, 1991; Poschlod, 2015). The absence of appropriate tools (such as scythes) in archaeological records from earlier periods is frequently cited as a main argument against the development of hay meadows prior to the Roman Iron Age (Hejcman et al., 2013). On the other hand, some authors suggest that the increasing diversity of grassland taxa in both archaeobotanical materials and pollen diagrams from earlier periods may indicate not only the development of pastures but also the initial formation of mown (cut) meadows in the Bronze Age and Early Iron Age (Greig, 1984, 1988; Küster, 1988; Speier, 1994). In field surveys, patches of pastures and mown meadows are easily distinguishable by differences in vegetation structure as well as physical properties of soil and ground relief. The problem arises when attempting to classify grassland species recorded in archaeobotanical samples as representing grazed (pastures) versus ungrazed (mown meadow) vegetation.

Grazing and mowing exert different pressures on vegetation, promoting or suppressing groups of species with specific functional traits. In recent years, several studies have attempted to identify the ecological factors and competitive mechanisms among grassland plants under different management methods, their intensities and exclusion (Augustine and McNaughton, 1998; Hodgson et al., 1999; Stammel et al., 2003; Poschlod et al., 2005; Klimešová et al., 2008; Tälle et al., 2016; Bonari et al., 2017; Swacha et al., 2018, 2023; Raduła et al., 2022; Reutimann et al., 2023; Sonnier et al., 2023). The main aim of these studies is to determine which management practices would be most effective in preventing the recent biodiversity loss observed in grassland vegetation across different geographic regions and grassland types. The results, based on field observations and analyses of functional traits of particular species and species groups – considered fundamental factors shaping their resistance and resilience under specific pressures – are also highly relevant for interpreting palaeodata. While these studies highlight the complexity of ecological processes in grasslands and sometimes yield conflicting results regarding the impact of particular management methods on plant fitness and species composition (Stammel et al., 2003; Schieltz and Rubenstein, 2016; Tälle et al., 2016), they provide strong reasons for caution when interpreting archaeobotanical finds of grassland taxa without an appropriate context (such as a bundle of hay or animal dung/manure). Importantly, several studies show that extensive livestock grazing does not significantly alter the local flora, maintaining species compositions similar to those of mown meadows (Pykälä, 2000). Furthermore, it should be considered that, at the early stages of semi-natural grassland development, a combination of mowing and grazing on the same plot was most probably applied. According to historical data, such farming systems were practiced in Europe up to the 19th century and are still maintained in some remote regions with traditional agriculture (Biró et al., 2020; Sucholas et al., 2022; Janišová et al., 2023).

The long list of taxa originating from grassland vegetation around the Polanowo, Grodno and Biskupin sites includes several species typically found in pastures as unpalatable plants due to specific chemical compounds (e.g. *Mentha* spp., *Ranunculus* spp., *Lycopus europaeus*, *Eupatorium cannabinum*) or structural defense traits (e.g. *Cirsium* spp., *Juncus* spp.). It also includes species tolerant of trampling and other disturbances by grazers, due to regeneration traits enabling rapid spread over disturbed ground, such as stem-derived clonal growth (*Agrostis stolonifera*, *Ranunculus repens*) or tillering (*Poa annua*). Typical pasture species also include rosette and semi-rosette forms (*Plantago media*, *P. major*) or prostrate plants (*Polygonum aviculare*) which grow close to the ground and can thus escape defoliation by grazers (Stammel et al., 2003). However, most taxa in our list are species that better develop in present-day traditionally mown meadows (Reutimann et al., 2023) and have been documented in various archaeobotanical records from the Roman Iron Age and Medieval period as potential or probable remnants of hay (Greig, 1983, 1988; Lodwick, 2017; Reed, 2024). These are mostly perennial, upright-growing forbs such as *Linum catharticum*, *Centaurea scabiosa*, *Leucanthemum vulgare*, *Achillea millefolium*, *Filipendula ulmaria*, *Lychnis flos-cuculi*, *Thalictrum flavum*, *Rumex acetosa*, *Pimpinella saxifraga*, *Leontodon autumnalis*, tussock grasses (*Deschampsia caespitosa*, *Molinia caerulea*), and plants developing underground storage organs (*Ranunculus bulbosus*, *Daucus carota*), which today grow in meadows across different habitats. It should be emphasized, however, that most grassland species are ecological generalists and, similar to the present-day situations, also in the past certainly occurred not only in different grassland communities under grazing and mowing regimes but also as weeds in ruderal habitats, among crops, and in fallows. Others were components of vegetation in forest glades and edges (e.g. *Primula veris*, *Clinopodium vulgare*, *Origanum vulgare*) or in natural wetlands (e.g. *Lycopus europaeus*, *Ranunculus sceleratus*, *Caltha palustris*), that is, natural habitats later transformed by livestock grazing and haymaking into semi-natural grasslands. Moreover, recent studies suggest that genetic and epigenetic variation in populations of some grassland species may be partly induced by different management-related disturbances (e.g. due to mowing and grazing), which may explain adaptation to grazing pressure in species such as *Plantago lanceolata* (Gáspár et al., 2019), *Linum catharticum* (Pagel et al., 2020), *Trifolium pratense* (Lehmair et al., 2022) and others. Therefore, following earlier statements by e.g. Behre and Jacomet (1991), the mere occurrence of grassland species in archaeobotanical materials without specific context is insufficient for reconstructing grassland management and should not be interpreted without supplementary archaeological information on animal husbandry and agricultural tools used by local populations.

Already in the Neolithic, grasses, reeds and sedges were certainly cut for many purposes such as roof thatching, insulation, bedding and even elements of clothing, as shown by botanical analyses related to the Iceman Ötzi (found in the Alps), who had a cap made of bundles of *Brachypodium pinnatum*, while hay consisting of several other grass species was used as insulating material in his shoes (Acs et al., 2005). However, the crucial factor in the context of the development of hay meadows was the increasing harvest of forbs and grasses for stable litter and animal fodder. Although several studies based on analyses of animal dung from Neolithic and Bronze Age sites in Europe provide firm evidence that tree leaves and twigs were the main winter fodder for livestock kept in stables (Rasmussen, 1989, 1993; Karg, 1998), some data also indicate that feeding animals with grass hay may have already occurred during these periods (Jakobitsch et al., 2023). Collecting grass hay with flint sickles or bare hands was certainly inefficient and likely restricted to small areas. Such activities would have had only limited influence on the formation of new plant communities.

In the Late Bronze and Early Iron Ages, new methods and tools were implemented in land management (Urban, 2019). Traditional livestock grazing in forests for most of the year, and the acquisition of winter fodder and stable litter through tree lopping and peeling, were certainly still in practice, as these methods are known to have continued into modern times (Halstead, 1998; Öllerer et al., 2019). But the distinctly rising share of open land and variation in grassland taxa illustrated by the pollen diagrams, as well as the presence of species typical for different grassland communities in the archaeobotanical samples, allow us to assume a variety of land management practices in a variety of habitats. Although flint sickles were still used by the LUC farmers, the much more effective bronze and then iron sickles were also known (Gackowski, 2016; Orlicka-Jasnoch, 2019; Urban, 2019; Gackowski and Rosołowski, 2022). The archaeological records present various types of these tools from LUC sites, including some large iron blades 20–30 cm long, which could be used in a similar way to the later short-handled scythes (summarized by Urban, 2019). Moreover, some flint sickles exhibit microscopic damage interpreted as traces of the contact with soil due to plant cutting close to the ground (Baron and Kufel-Diakowska, 2013). Therefore, we may expect that the sickles used by LUC farmers served not only for harvesting cereals, but potentially also for collecting hay.

The important arguments for the discussion on potential haymaking by the LUC farmers come from archaeozoological data. In general, remains of animal bones from LUC settlements indicate a very low share of game, which means that breeding livestock was a major source of meat, while hunting was of minor importance in the economy of this culture (Rembisz et al., 2009; Gocman, 2020, 2021). Cattle were of primary importance, usually followed by sheep/goats or pigs in second or third place (Piątkowska-Małecka, 1999; Gocman, 2021). The archaeozoological data from Grodno (Piątkowska-Małecka, 1999) and Polanowo (Gręzak, 2010) follow the pattern seen at other LUC sites. Cattle were mainly kept for meat, but there is also evidence for the use of oxen (Rembisz et al., 2009). The growing number of ceramic sieves found in archaeological excavations related to this culture (Urban, 2019) seems to indicate milk processing. Measurements of livestock bones at all sites show that adult animals were of low or medium height, which may suggest either a shortage of winter food or poor-quality fodder (Gręzak, 2010). Ruminants are able to extract nutrients effectively from a wide range of fodder, including that with high fiber content, which means that tree leaf and twig fodder provided by farmers, or browsing on shrubs and tree twigs in winter, could be sufficient to meet survival needs during the off-growing season (Hejcman et al., 2014). In the study area, livestock also had access to wetlands, which could be grazed in winter (Kulik et al., 2023). It, however, remains a question whether such foddering, without supplementary herbaceous hay, was sufficient for cattle reproduction, milk production, and the good performance of draught animals. The share of horse bones varies among LUC sites, usually remaining below 10% (Gocman, 2020); but, for example, at the Ruda site (Rembisz et al., 2009), it reaches up to 19% of the total identified bone specimens, ranking second after cattle. At this site, most of the horses were 6–8 years old when they were slaughtered for meat, but some lived up to 15–16 years, which indicates their importance and use for purposes other than food. The increasing number of horse bridle elements found among metal hoards at LUC sites in north-central Poland (including Grodno) suggests the use of saddle horses in the Final Bronze Age in the region (Gackowski et al., 2023). According to experiments by Menard et al. (2002), horses eat up to 63% more forage than cattle, because they are less efficient than ruminants at digesting plant material with high fiber content. They tend to eat mainly grass, compensating for its poor nutritional value with higher intake (Duncan et al., 1990). Grass fodder is necessary for horse welfare and long-term survival, while tree fodder may be used as a supplement, excluding species that are poisonous or harmful to equines. Therefore, it is justified to propose that grass hay must have been used for horse breeding, at least in the later LUC settlements.

Livestock breeding required large amounts of fodder. In warm seasons, animals were grazed in forests, wetlands, stubble fields after harvest, fallows, and on patches of pasture that, according to our data, certainly existed around the settlements. The question that remains open is how livestock was fed in winter. Was the livestock grazed year-round outside settlements without any, or with only limited supplementary feeding, as suggested by Hejcman et al. (2014), or was it kept and fed with leaf fodder or hay in settlements for at least part of the winter season? Given the location of Poland in the temperate continental humid zone, the first scenario would be possible except during prolonged harsh winters, which could, however, have occurred during the time the settlements in Polanowo, Grodno and Biskupin were occupied. A large amount of data illustrates abrupt global climate cooling ~2,800–2,450 years cal. BP, commonly referred to as the 2.8 ka event or the Homeric Climate Anomaly (e.g. Van Geel et al., 1996; Wanner et al., 2011; Martin-Puertas et al., 2012; García et al., 2024), which is also well documented in Polish paleolimnological records (Pleskot et al., 2018; Tylmann et al., 2024). The climate deterioration prompted many forms of socioeconomic adaptation to environmental changes, including shifts in agricultural systems (Van Geel et al., 2004; Tipping et al., 2008; Turney et al., 2016; Madgwick et al., 2023). Therefore, this supports the argument for providing fodder for livestock housed within settlements in the study regions. Some authors also emphasize that stabling livestock was important as a source of manure for fertilizing arable fields (Lasota-Moskalewska, 1991). In fact, functional reconstructions of houses in LUC settlements indicate that animals were most likely kept in a dedicated space within the house (Biskupin; Dzięgielewski, 2017) or in a type of outbuilding (Ruda; Rembisz, 2011). In turn, at Grodno, analyses of phosphorus content in soil suggest that animals may have been kept in the central part of the settlement (construction unknown), as indicated by very high levels of this element (Bednarek and Markiewicz, 2009). There is ample literature on the manuring of fields as early as the Neolithic (Bogaard et al., 2013), and later in the Bronze Age and Early Iron Age (Nielsen et al., 2019; Hald et al., 2024). Unfortunately, there is no direct archaeobotanical evidence of field manuring in the Late Bronze and Early Iron Age from the area of Poland, but such an assumption may be drawn from the field weed ecological spectra showing a high representation of nitrophilous species in sub-fossil samples of cultivated plants from these periods (Lityńska-Zając, 2005). Also, analyses of dung and manure have not been conducted on archaeological features from LUC sites in Poland, and the same applies to features that could have served for winter fodder storage. Archaeologists describe various storage objects and constructions discovered at LUC sites (summarized by Urban, 2019). The majority were used to store cereal grain and other crops, but some features are interpreted as likely remnants of haystacks. Traces of such constructions are known from Biskupin and several other LUC sites (Urban, 2019) and may be accepted as additional support for haymaking.

CONCLUSIONS

In contrast to large number of pollen data reflecting a distinct opening of the landscape and the development of various types of non-forest vegetation in areas inhabited by the LUC tribes at the transition from the Late Bronze Age to the Early Iron Age, data based on plant macrofossils focused on vegetation surrounding LUC sites remain scarce. The present study is the second from Poland (after the earlier one from Biskupin; Jaroń, 1938), based on waterlogged remains, revealing a long list of plant taxa (239) from various habitats. The development of grasslands and their potential management during the late LUC occupation were the main subjects of this paper, enabling the formulation of the following conclusions:

1 – The broad list of grassland taxa, including species characteristic of habitats ranging from wetlands to semi-dry and dry ones, indicates that the LUC farmers exploited all available environments around their settlements.

2 – Gradual thinning of various forest types and further use of these grounds for crop cultivation and livestock grazing led to the spread of forbs and grasses with functional traits enabling their populations to expand under pressure from LUC land use. Our data suggest that diverse, semi-natural grassland communities, referring to both wet and mesic vegetation – now classified as *Molinio-Arrhenatheretea*, semi-dry grasslands (*Festuco-Brometea*) and poor swards (mainly *Nardo-Callunetea*) – began to develop at that time.

3 – The large representation of species typical of heavily trampled grounds enriched by nitrogen compounds indicates a high level of LUC settlers' activity around both study sites.

4 – Although our data are based on the analysis of a relatively low number of samples, the qualitative and quantitative richness of the subfossil materials partially compensates for this limitation. This is supported by the distribution of edaphic factors for grassland taxa, which illustrates differences in habitat conditions between the sites, consistent with recent maps of potential vegetation.

5 – The thanatocoenose character of the material presented in this study precludes reconstructing grassland management methods used by the LUC farmers solely from archaeobotanical evidence. However, combining data on the occurrence of several species common in traditionally mown meadows with archaeological findings of metal sickles potentially used for hay cutting and archaeozoological data indicating the importance of livestock (including horse breeding) in LUC settlements justifies the hypothesis of grass hay collecting.

6 – Plant remains filling the vessels from Grodno and Polanowo originate from various vegetation types and largely resemble the botanical contents of cultural layers accumulating in waterlogged settlement sites. However, the unexpectedly large proportions of *Chenopodium album* seeds and numerous seeds of *Camelina sativa* and *Papaver somniferum* in both vessels from Polanowo allow us to suggest that some plant material could have been deliberately put in these vessels as an element of foundation offerings.

Our study affords new archaeobotanical data important for the knowledge on the environmental context of the LUC settlement development in the Early Iron Age, in the northern part of Central Poland, and on its impact on vegetation. It also highlights the importance of careful analysis of botanical contents of vessels found at archaeological sites, not only when the presence of large seeds and fruits is recognized by the naked eye. The use of plants in magical contexts across different ancient cultures and regions is a fascinating subject that can be studied by combining archaeobotany and archaeology. This study also offers insights into the early history of European semi-natural grasslands from a geographic region still poor in such evidence.

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AUTHORS CONTRIBUTION. KM carried out the analysis of plant macroremains (Grodno), discussed the concept of the article, compiled all the results, worked out all of the technical details (database, tables and figures), made statistical analyses, provided the early draft of the manuscript, reviewed and discussed its final version; ML discussed the concept of the article, carried out the analysis of plant macroremains (Polanowo), wrote the manuscript with the support from KM; DK carried out the analysis of plant macroremains and compiled a part of the results from Grodno; MB coordinated the study, discussed the concept of the article, revised determinations of plant macroremains (Grodno), and reviewed all drafts of the manuscript. We provided all of the data for this manuscript and agree to its publication.

REFERENCES

Abraham, V., Kuneš, P., Petr, L., Svitavská-Svobodová, H., Kozáková, R., Jamrichová, E., Švarcová, M.G., Pokorný, P., 2016. A pollen-based quantitative reconstruction of the Holocene vegetation updates a perspective on the natural vegetation in the Czech Republic and Slovakia. Preslia 88, 409–434.

Acs, P., Wilhalm, T., Oeggl, K., 2005. Remains of grasses found with the Neolithic Iceman "Ötzi". Vegetation History and Archaeobotany 14, 198–206. https://doi.org/10.1007/s00334-005-0014-x

Akeret, Ö., Kiefer, S., Kühn, M., Rentzel, P., Rösch, M., Wick, L., 2018. The buried medieval pasture of Onoldswil (Niederdorf BL, Switzerland, AD 1295): an example of a well preserved palaeobiocoenosis. Vegetation History and Archaeobotany 27, 137–149. https://doi.org/10.1007/s00334-017-0623-1

Augustine, D.J., McNaughton, S.J., 1998. Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance. The Journal of Wildlife Management 62(4), 1165–1183. https://doi.org/10.2307/3801981

Badura, M., Noryśkiewicz, A.M., Chudziak, W., Kaźmierczak, R., 2018. Environmental context and the role of plants at the early medieval artificial island in the lake Paklicko Wielkie, Nowy Dworek, western Poland. Vegetation History and Archaeobotany 27, 99–110. https://doi.org/10.1007/s00334-017-0617-z

Baron, J., 2012. Ritual and cultural change. Transformations in rituals at the junction of pagan religion and Christianity in early medieval Poland. In: Gediga, B., Grossman, A., Piotrowski, W. (eds), Rytm przemian kulturowych w pradziejach i średniowieczu, Biskupin-Wrocław, pp. 449–464.

Baron, J., Kufel-Diakowska, B., 2013. Deposit of bifacial flint sickles from a late Bronze Age settlement in Korczowa, SE Poland. In: Kolenda, J., Mierzwiński, A., Moździoch, S., Żygadło, L. (eds), Z badań nad kulturą społeczeństw pradziejowych i wczesnośredniowiecznych: księga jubileuszowa dedykowana Profesorowi Bogusławowi Gedidze, w osiemdziesiątą rocznicę urodzin przez przyjaciół, kolegów i uczniów, Wrocław, pp. 567–574.

Bednarek, R., Markiewicz, M., 2009. Ślady zabudowy osady obronnej ludności kultury łużyckiej w Grodnie, gm. Chełmża (stanowisko 6) na podstawie zawartości fosforu. (Traces of buildings of the Lusatian Culture people's defensive settlement in Grodno, Chełmża commune (site 6) on the base of phosphorus contents analysis). In: Gackowski, J. (ed.), Archeologia epok brązu i żelaza. Studia i materiały Vol. 1. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 257–265.

Beer, J., Van Geel, B., 2008. Holocene Climate Change and the Evidence for Solar and other Forcings. In: Battarbee, R.W., Binney, H.A. (eds), Natural Climate Variability and Global Warming: A Holocene Perspective, Blackwell Publishing Ltd, pp. 138–162. https://doi.org/10.1002/9781444300932.ch6

Behre, K.-E., 1976. Die Pflanzenreste Aus Der Fruehgeschichtlichen Wurt Elisenhof.Die ftiihgeschichtliche Marschensiedlung beim Elisenhof in Fiderstedt. Band 2. Herbert Lang, Bern.

Behre, K.-E., 2008. Collected seeds and fruits from herbs as prehistoric food. Vegetation History and Archaeobotany 17, 65–73. https://doi.org/10.1007/s00334-007-0106-x

Behre, K.-E., Jacomet, S., 1991. The ecological interpretation of archaeobotanical data. In: Van Zeist, W., Wasylikowa, K., Behre, K.-E. (eds), Progress in Old World palaeoethnobotany. Balkema, Rotterdam, pp. 81–108.

Berglund, B.E., 1991. The Cultural Landscape during 6000 Years in Southern Sweden: the Ystad Project. Ecological bulletins 41. Copenhagen. Munksgaard International Booksellers and Publishers.

Bevan, A., Colledge, S., Fuller, D., Fyfe, R., Shennan, S., Stevens, C., 2017. Holocene fluctuations in human population demonstrate repeated links to food production and climate. Proceedings of the National Academy of Sciences 114(49), E10524-E10531. https://doi.org/10.1073/pnas.1709190114

Bieniek, A., 2002. Archaeobotanical analysis of some Early Neolithic settlements in the Kujawy region, central Poland, with potential plant gathering activities emphasised. Vegetation History and Archaeobotany 11(1–2), 33–40. https://doi.org/10.1007/s003340200004

Biró, M., Molnár, Z., Öllerer, K., Lengyel, A., Ulicsni, V., Szabados, K., Kiš, A., Perić, R., Demeter, L., Babai, D., 2020. Conservation and herding co-benefit from traditional extensive wetland grazing. Agriculture, Ecosystems & Environment 300, 106983. https://doi.org/10.1016/j.agee.2020.106983

Bishop, R.R., Church, M.J., Rowley-Conwy, P.A., 2015. Firewood, food and human niche construction: the potential role of Mesolithic hunter-gatherers in actively structuring Scotland's woodlands. Quaternary Science Reviews 108, 51–75. https://doi.org/10.1016/j.quascirev.2014.11.004

Bogaard, A., 2004. Neolithic farming in central Europe: an archaeobotanical study of crop husbandry practices. London. Routledge.

Bogaard, A., Fraser, R., Heaton, T.H.E., Wallace, M., Vaiglova, P., Charles, M., Jones, G., Evershed, R.P., Styring, A.K., Andersen, N.H., Arbogast, R.M., Bartosiewicz, L., Gardeisen, A., Kanstrup, M., Maier, U., Marinova, E., Ninov, L., Schäfer, M., Stephan, E., 2013. Crop manuring and intensive land management by Europe's first farmers. Proceedings of the National Academy of Sciences 110(31), 12589–12594. https://doi.org/10.1073/pnas.1305918110

Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uřičář, J., Chytrý, M., 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. Agriculture, Ecosystems & Environment 246, 243–252. https://doi.org/10.1016/j.agee.2017.06.010

Brzeg, A., Wojterska, M., 2001. Zespoły roślinne Wielkopolski, ich stan poznania i zagrożenie. In: Wojterska, M. (ed.), Szata roślinna Wielkopolski i Pojezierza Południowopomorskiego, Przewodnik sesji terenowych 52 Zjazdu PTB, 24–28 września 2001, pp. 39–110. (in Polish)

Bush, M.B., 1993. An 11 400 Year Paleoecological History of a British Chalk Grassland. Journal of Vegetation Science 4(1), 47–66. https://doi.org/10.2307/3235733

Cappers, R.T.J., Bekker, R.M., Jans, J.E.A., 2012. Digital seed atlas of the Netherlands. Barkhuis. Groningen University Library.

Ceynowa, M., 1968. Zbiorowiska roślinności kserotermicznej nad Dolną Wisłą (summary: Xerotherme Pflanzengesellschaften an der unteren Wisła). Studia Societatis Scientiarum Torunensis. Sectio D, Botanica 8(4), 155.

Chabuz, W., Kulik, M., Sawicka-Zugaj, W., Żółkiewski, P., Warda, M., Pluta, M., Lipiec, A., Bochniak, A., Zdulski, J., 2019. Impact of the type of use of permanent grasslands areas in mountainous regions on the floristic diversity of habitats and animal welfare. Global Ecology and Conservation 19, e00629. https://doi.org/10.1016/j.gecco.2019.e00629

Chmiel, J., Nowak, B., Gezella-Nowak, I., 2019. Rośliny naczyniowe Jeziora Powidzkiego i jego okolic. In: Nowak, B. (ed.), Jezioro Powidzkie wczoraj i dziś. Instytut Meteorologii i Gospodarki Wodnej – Państwowy Instytut Badawczy, Warszawa, pp. 75–98.

Chytrý, M., Řezníčková, M., Novotný, P., Holubová, D., Preislerová, Z., Attorre, F., Biurrun, I., Blažek, P., Bonari, G., Borovyk, D., Čeplová, N., Danihelka, J., Davydov, D., Dřevojan, P., Fahs, N., Guarino, R., Güler, B., Hennekens, S.M., Hrivnák, R., Kalníková, V., Kalusová, V., Kebert, T., Knollová, I., Knotková, K., Koljanin, D., Kuzemko, A., Loidi, J., Lososová, Z., Marcenò, C., Midolo, G., Milanović, D., Mucina, L., Novák, P., von Raab-Straube, E., Reczyńska, K., Schaminée, J.H.J., Štěpánková, P., Świerkosz, K., Těšitel, J., Těšitelová, T., Tichý, L., Vynokurov, D., Willner, S., Axmanová, I., 2024. FloraVeg.EU – an online database of European vegetation, habitats and flora. Applied Vegetation Science 27, e12798. Available from: https://doi.org/10.1111/avsc.12798 (https://floraveg.eu/. Accessed March 2025).

Ciaraldi, M., Richardson, J., 2000. Food, Ritual and Rubbish in the Making on Pompeii. Theoretical Roman Archaeology Journal 1999, 74–82. https://doi.org/10.16995/TRAC1999_74_82

Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Erhardt, A., Baur, B., 2005. Alterations of Steppe-Like Grasslands in Eastern Europe: a Threat to Regional Biodiversity Hotspots. Conservation Biology 19(5), 1606–1618. https://doi.org/10.1111/j.1523-1739.2005.00084.x

Czerniak, L., Święta-Musznicka, J., Pędziszewska, A., Goslar, T., Matuszewska, A., 2023. Palynological studies shed new light on the Neolithisation process in central Europe. Journal of Anthropological Archaeology 70, 101513. https://doi.org/10.1016/j.jaa.2023.101513

Dalewski, Z., 1990. Zakładziny: obrzęd i mit. O słowiańskich zwyczajach i wierzeniach związanych z budową domu i zakładaniem miasta. Polska Sztuka Ludowa. Konteksty 44(4), 17–24.

Davidson, N.C., 2014. How Much Wetland Has the World Lost? Long-Term and Recent Trends in Global Wetland Area. Marine and Freshwater Research 65(10), 934–941. https://doi.org/10.1071/MF14173

Dąbrowski, J., 2009. Polska przed trzema tysiącami lat: czasy kultury łużyckiej (summary: (Poland three thousand years ago: the Lusatian Culture and his times). Wydawnictwo Trio. Warszawa.

Dietze, E., Theuerkauf, M., Bloom, K., Brauer, A., Dörfler, W., Feeser, I., Feurdean, A., Gedminienė, L., Giesecke, T., Jahns, S., Karpińska-Kołaczek, M., Kołaczek, P., Lamentowicz, M., Latałowa, M., Marcisz, K., Obremska, M., Pędziszewska, A., Poska, A., Rehfeld, K., Stančikaitė, M., Stivrins, N., Święta-Musznicka, J., Szal, M., Vassiljev, J., Veski, S., Wacnik, A., Weisbrodt, D., Wiethold, J., Vannière, B., Słowiński, M., 2018. Holocene fire activity during low-natural flammability periods reveals scale-dependent cultural human-fire relationships in Europe. Quaternary Science Reviews 201, 44–56. https://doi.org/10.1016/j.quascirev.2018.10.005

Divišová, M., Šida, P., 2015. Plant Use in the Mesolithic Period. Archaeobotanical Data from Czech Republic in a European Context – a Review. Interdisciplinaria Archaeologica. Natural Sciences in Archaeology 6(1), 95–106. https://doi.org/10.24916/iansa.2015.1.7

Dufraisse, A., 2008. Firewood management and woodland exploitation during the late Neolithic at Lac de Chalain (Jura, France). Vegetation History and Archaeobotany 17, 199–210. https://doi.org/10.1007/s00334-007-0098-6

Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G., Lloyd, M., 1990. Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. Oecologia 84, 411–418. https://doi.org/10.1007/BF00329768

Dzięgielewski, K., 2017. The rise and fall of Biskupin and its counterparts. In: Bugaj, U. (ed.), The past societies: Polish lands from the first evidence of human presence to the Early Middle Ages (Vol. 3).

Instytut Archeologii i Etnologii Polskiej Akademii Nauk. Warszawa, pp. 342–366.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18. Goltze, Göttingen 18, 2nd ed.

Eriksson, O., Cousins, S.A.O., 2014. Historical Landscape Perspectives on Grasslands in Sweden and the Baltic Region. Land 3(1), 300–321. https://doi.org/10.3390/land3010300

European Pollen Database 2007–2025. Available from: https://www.europeanpollendatabase.net/. Accessed March 2025.

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S.M., Hickler, T., 2018. Biodiversity-rich European grasslands: ancient, forgotten ecosystems. Biological Conservation 228, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022

Filbrandt-Czaja, A., 1998. Holoceńska historia roślinności północnej części Lednickiego Parku Krajobrazowego ze szczególnym uwzględnieniem czynnika antropogenicznego (summary: The Holocene history of vegetation of the northern part of Lednica Landscape Park with the special allowance of anthropogenic factor). In: Tobolski, K. (ed.), Biblioteka Studiów Lednickich 3, Muzeum Pierwszych Piastów na Lednicy. Poznań, pp. 9–42.

Filbrandt-Czaja, A., 2009. Historia działalności człowieka w rejonie Jeziora Grodzieńskiego koło Chełmży w świetle analizy pyłkowej (summary: History of human activities in the vicinity of Grodno Lake near Chełmża in the light of pollen analysis). In: Gackowski, J. (ed.), Archeologia epok brązu i żelaza. Studia i materiały t. 1. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 233–256.

Filipek, M., 1974. Xerothermic swards of the Lower Odra and Warta region. The Poznań Society of Friends of Art and Sciences, Biological Letters 38, 1–109.

Fitzke, J., 1938/1939. Próba rekonstrukcji wyglądu domu w grodzie kultury łużyckiej w Biskupinie (Essai reconstitution d’une maison de l’enceinte fortifiée de la civilisation lusacienne à Biskupin). Przegląd Archeologiczny 6(2–3), 258–261. (in Polish)

FloraVeg.EU. https://floraveg.eu/. Accessed March 2025.

Fyfe, R.M., Woodbridge, J., Roberts, N., 2015. From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. Global Change Biology 21(3), 1197–1212. https://doi.org/10.1111/gcb.12776

Gackowski, J., Rosołowski, S., 2022. Skarby przedmiotów metalowych z młodszej epoki brązu i wczesnej epoki żelaza w regionie kujawsko-pomorskim (Metal hoards from the region of Kuyavia and Pomerania during the Late Bronze Age and Early Iron Age). In: Gackowski, J., Gawiński, S., Sosnowski, M., Dąbrowski, H.P. (eds), Pradziejowe cymelia województwa kujawsko-pomorskiego Skarby ludności kultury łużyckiej z Brudzynia, Cierpic i Elgiszewa. Wydawnictwo Towarzystwa Naukowego w Toruniu, pp. 13–22.

Gackowski, J., 2003. Uwagi o niektórych materiałach zabytkowych z osiedla obronnego kultury łużyckiej w Grodnie koło Chełmży (na podstawie wyników badań z lat 1997–2001) (summary: Anmerkungen über historisches Material aus einer Wehrsiedlung der Lausitzer Kultur in Grodno bei Chełmża (auf Grundlage von Untersuchungen aus den Jahren 1997–2000)). In: Fudziński, M., Paner, H. (eds), XIII Sesja Pomorzoznawcza. Vol. 1, Od epoki kamienia do okresu rzymskiego. Muzeum Archeologiczne w Gdańsku, Gdańsk, pp. 105–115.

Gackowski, J., 2009. Osada obronna z początku epoki żelaza w Grodnie koło Chełmży w świetle dotychczasowych odkryć (summary: Eine befestigte Siedlung vom Beginn der Eisenzeit in Grodno bei Chełmża im Lichte bisheriger Entdeckungen). In: Fudziński, M., Paner, H., Czopka, S. (eds), Nowe materiały kultury łużyckiej i pomorskiej z Pomorza. Muzeum Archeologiczne, Gdańsk, pp. 25–36.

Gackowski, J., 2010 (unpubl.). Sprawozdanie z badań archeologicznych przeprowadzonych w 2010 roku w miejscowości Mirakowo-Grodno, gm. Chełmża, na stan. 6 (obszar AZP 37–44: 15). Archives Wojewódzki Urząd Ochrony Zabytków w Toruniu i archiwum Katedry Prahistorii IA UMK w Toruniu), Toruń.

Gackowski, J., 2016. The Younger Bronze Age and the Beginning of the Iron Age in Chełmno Land in the Light of the Evaluation of Selected Finds of Metal Products. Analecta Archaeologica Ressoviensia 11, 165–207. https://doi.org/10.15584/anarres.2016.11.8

Gackowski, J., Kowalski, Ł., Garbacz-Klempka, A., Rembisz-Lubiejewska, A., Noryśkiewicz, A., Kamiński, D., Podgórski, A., Szczepańska, G., Molewski, P., Sosnowski, M., Kołyszko, M., Kozicka, M., Sokół, A., 2023. A Final Bronze Age hoard from Cierpice, Poland: new evidence for the use and deposition of a horse bridle in the region. Praehistorische Zeitschrift 98(2), 646–674. https://doi.org/10.1515/pz-2023-2018

García, M.L., Birlo, S., Zahajská, P., Wienhues, G., Grosjean, M., Zolitschka, B., 2024. Ecological responses to solar forcing during the Homerian Climate Anomaly recorded by varved sediments from Holzmaar, Germany. The Holocene 34(12), 1752–1764. https://doi.org/10.1177/09596836241275008

Gáspár, B., Bossdorf, O., Durka, W., 2019. Structure, stability and ecological significance of natural epigenetic variation: a large-scale survey in *Plantago lanceolata*. New Phytologist 221(3), 1585–1596. https://doi.org/10.1111/nph.15487

Gocman, U., 2020. Evaluation of the animal husbandry economy and meat consumption in the early and classical developmental phases of the Lusatian culture in Witów, 1, Koszyce commune. Przegląd Archeologiczny 68, 47–72. https://doi.org/10.23858/PA68.2020.003

Gocman, U., 2021. Livestock Subsistence Strategies in the Middle and Late Bronze Age Lesser Poland.

Environmental Archaeology 28(4), 228–239. https://doi.org/10.1080/14614103.2021.1953936

Gołaszewska, E., Gadziszewska, J., Latałowa, M., 2019. First record of orchid subfossil seeds – The abundant occurrence of *Epipactis palustris* (L.) Crantz and *Dactylorhiza* spp. seeds in early Holocene sediments from Central Europe. Review of Palaeobotany and Palynology 265, 1–12. https://doi.org/10.1016/j.revpalbo.2019.03.001

Góralczyk, A., 2024. Podstawy datowania grodów kultury łużyckiej na Ziemiach Polskich (Basics of dating Lusatian culture defensive settlements in the polish lands). Folia Praehistorica Posnaniensia 29, 57–88. https://doi.org/10.14746/fpp.2024.29.04

Gradmann, R., 1933. Die Steppenheidetheorie. Geographische Zeitschrift 39(5), 265–278.

Grange, G., Finn, J.A., Brophy, C., 2021. Plant diversity enhanced yield and mitigated drought impacts in intensively managed grassland communities. Journal of Applied Ecology 58(9), 1864–1875. https://doi.org/10.1111/1365-2664.13894

Greig, J., 1983. The archaeobotanical remains of hay: a comparison of results from seven DoE sites and various others with data obtained from species-rich "Ancient meadows". Ancient Monuments Laboratory Report 4077, 13.

Greig, J., 1984. The palaeoecology of some British hay meadow types. In: Van Zeist, W., Casparie, W.A. (eds), Plants and Ancient Man, Studies in Palaeoethnobotany. A. A. Balkema, Rotterdam, pp. 213–226.

Greig, J., 1988. Some evidence of the development of grassland plant communities. In: Jones, M. (ed.), Archaeology and the Flora of the British Isles. Oxford University Committee for Archaeology Monograph 14, Oxford, pp. 39–52.

Gręzak, A., 2010. Analiza zwierzęcych szczątków kostnych z pozostałości osad ludności łużyckich pól popielnicowych w Polanowie i Powidzu na Pojezierzu Gnieźnieńskim (abstract: Analysis of animal bone remains from the Lusatian Urnfield Culture settlements in Polanowo and Powidz in the Gniezno Lake District). In: Pydyn, A. (ed.) Archeologia Jeziora Powidzkiego. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 227–245.

Habel, J.Ch., Dengler, J., Janišová, M., Török, P., Wellstein, C., Wiezik, M., 2013. European grassland ecosystems: threatened hotspots of biodiversity. Biodiversity and Conservation 22, 2131–2138. https://doi.org/10.1007/s10531-013-0537-x

Hald, M.M., Styring, A., Mortensen, M.F., Maltas, T., Vidas, D., Henriksen, P.S., Pihl, A., Jensen, P.M., Christensen, L.B., Hansen, J., Dollar, S., Egeberg, T., Lundø, M.B., Haue, N., Hertz, E., Iversen, R.B., Jørgensen, T., Kristensen, I.K., Klassen, L., Møller, N.A., Pedersen, V.J., Ravn, M., Vestergaard, K., Jessen, M.D., 2024. Farming during turbulent times: Agriculture, food crops, and manuring practices in Bronze Age to Viking Age Denmark. Journal of Archaeological Science: Reports 58, 104736. https://doi.org/10.1016/j.jasrep.2024.104736

Halstead, P., 1998. Ask the fellows who lop the hay: leaf-fodder in the mountains of northwest Greece. Rural History 9(2), 211–234. https://doi.org/10.1017/S0956793300001588

Hanisch, M., Schweiger, O., Cord, A.F., Volk, M., Knapp, S., 2020. Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. Journal of Applied Ecology 57(8), 1535–1550. https://doi.org/10.1111/1365-2664.13644

Hejcman, M., Hejcmanová, P., Pavlů, V., Beneš, J., 2013. Origin and history of grasslands in Central Europe – a review. Grass and Forage Science 68(3), 345–363. https://doi.org/10.1111/gfs.12066

Hejcman, M., Hejcmanová, P., Stejskalová, M., Pavlů, V., 2014. Nutritive value of winter-collected annual twigs of main European woody species, mistletoe and ivy and its possible consequences for winter foddering of livestock in prehistory. The Holocene 24(6), 659–667. https://doi.org/10.1177/0959683614526904

Helbaek, H., 1959. Comment on *Chenopodium album* as a food plant in prehistory. Berichte des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel 31, pp. 16–19. https://doi.org/10.5169/seals-377581

Heske, I., Lüth, P., Posselt, M., 2012. Deponierungen, Gargruben und ein verfüllter Wasserlauf. Zur Infrastruktur der Hünenburg-Außensiedlung bei Watenstedt, Lkr. Helmstedt. Vorbericht über die Grabung 2011. Praehistorische Zeitschrift 87(2), 308–337. https://doi.org/10.1515/pz-2012-0018

Hilczer-Kurnatowska, Z., 1982. Zakładziny. In: Labuda, G., Stieber, Z. (eds), Słownik Starożytności Słowiańskich. Encyklopedyczny zarys kultury Słowian od czasów najdawniejszych do schyłku wieku XII. Tom 7, Y-Ż, Zakład Narodowy Imienia Ossolińskich Wydawnictwo Polskiej Akademii Nauk, Wrocław, Warszawa, Kraków, Gdańsk. Łódź, pp. 52–54. (in Polish)

Hodgson, J.G., Halstead, P., Wilson, P.J., Davis, S., 1999. Functional interpretation of archaeobotanical data: making hay in the archaeological record. Vegetation History and Archaeobotany 8, 261–271. https://doi.org/10.1007/BF01291778

Horáčková, J., Podroužková, S., Juričková, L., 2023. Holocene transformation of natural steppe into an agricultural landscape in the Polabí and Pojizeří Lowlands, Czech Republic, based on mollusc evidence. The Holocene 34(1), 109–119. https://doi.org/10.1177/09596836231200441

Jacomet, S., Ebersbach, R., Akeret, Ö., Antolín, F., Baum, T., Bogaard, A., Brombacher, C., Bleicher, N.K., Heitz-Weniger, A., Hüster-Plogmann, H., Gross, E., Kühn, M., Rentzel, P., Steiner, B.L., Wick, L., Schibler, J.M., 2016. On-site data cast doubts on the hypothesis of shifting cultivation in the late Neolithic (c. 4300–2400 cal. BC): Landscape management as an alternative paradigm. The Holocene 26(11), 1858–1874. https://doi.org/10.1177/0959683616645941

Jakobitsch, T., Dworsky, C., Heiss, A.G., Kühn, M., Rosner, S., Leskovar, J., 2023. How animal dung can help to reconstruct past forest use: a late Neolithic case study from the Mooswinkel pile dwelling (Austria). Archaeological and Anthropological Sciences 15, 20. https://doi.org/10.1007/s12520-023-01724-5

Jamrichová, E., Libor, P., Jiménez-Alfaro, B., Jankovská, V., Dudová, L., Pokorný, P., Kołaczek, P., Zernitskaya, V., Čierniková, M., Břízová, V., Syrovátka, V., Hájková, P., Hájek., 2017. Pollen-inferred millennial changes in landscape patterns at a major biogeographical interface within Europe. Journal of Biogeography 44(10), 2386–2397. https://doi.org/10.1111/jbi.13038

Janišová, M., Bartha, S., Kiehl, K., Dengler, J., 2011. Advances in the conservation of dry grasslands: Introduction to contributions from the seventh European Dry Grassland Meeting. Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology 145(3), 507–513. https://doi.org/10.1080/11263504.2011.603895

Janišová, M., Bojko, I., Ivaşcu, C.M., Iuga, A., Biro, A-S., Magnes, M., 2023. Grazing hay meadows: History, distribution, and ecological context. Applied Vegetation Science, Special Issue: Grazing and Vegetation. Applied Vegetation Science 26(2), e12723. https://doi.org/10.1111/avsc.12723

Jaroń, B., 1938. Szczątki roślinne z wczesnego okresu żelaznego w Biskupinie (Wielkopolska) (summary: Les trouvailles botaniques de la cité "lusacienne" du premier âge du fer à Biskupin). In: Kostrzewski, J. (ed.), Gród prasłowiański w Biskupinie w powiecie żnińskim. Sprawozdanie z badań w latach 1936 i 1937 z uwzględnieniem wyników z lat 1934–1935, Poznań, pp. 1–30.

Kaczmarek, M., 2017. The Snares of Ostensible Homogenity. Lusatian Culture or Lusatian Urnfields? In: Bugaj, U. (ed.), The Past Societies 3. Polish lands from the first evidence of human presence to the Early Middle Ages: 2000–500 BC. Instytut Archeologii i Etnologii PAN, Warszawa, pp. 264–293.

Kahmen, S., Poschlod, P., 2008. Effects of grassland management on plant functional trait composition. Agriculture, Ecosystems and Environment 128(3), 137–145. https://doi.org/10.1016/j.agee.2008.05.016

Kajkowski, K., 2022. Ofiara zakładzinowa w świecie wczesnośredniowiecznych wyobrażeń zachodnio-słowiańskich (na przykładzie odkryć z ziem polskich). In: Dzik, M., Gogosz, R., Morawiec, J., Poniewozik, L. (eds), W świecie bogów, ludzi i zwierząt Studia ofiarowane Profesorowi Leszkowi Pawłowi Słupeckiemu. Wydawnictwo Uniwersytetu Rzeszowskiego, Rzeszów, pp. 407–433. (in Polish)

Kajtoch, Ł., Cieślak, E., Varga, Z., Paul, W., Mazur, M.A., Sramkó, G., Kubisz, D., 2016. Phylogeographic patterns of steppe species in Eastern Central Europe: a review and the implications for conservation. Biodiversity and Conservation 25, 2309–2339. https://doi.org/10.1007/s10531-016-1065-2

Karg, S., 1998. Winter- and Spring-foddering of Sheep/Goat in the Bronze Age Site of Fiavè-Carera, Northern Italy. Environmental Archaeology 1(1), 87–94. https://doi.org/10.1179/env.1996.1.1.87

Kącki, Z., Swacha, G., Lengyel, A., Korzeniak, J., 2020. Formalized Hierarchically Nested Expert System for Classification of Mesic and Wet Grasslands in Poland. Acta Societatis Botanicorum Poloniae 89(4), 8941. https://doi.org/10.5586/asbp.8941

Klichowska, M., 1964. Wyniki badań próbek botanicznych z wczesnośredniowiecznego stanowiska w Bonikowie, pow. Kościan, z 1958 r. Sprawozdania Archeologiczne 16, 413–414.

Klimat IMGW-PIB 2025. Aavailable from: https://klimat.imgw.pl. Accessed March 2025.

Klimešová, J., Latzel, V., de Bello, F., Van Groenendael, J.M., 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. Preslia 80, 245–253.

Kluk, K., 1805. Dykcyonarz roślinny, vol. I. Drukarnia Księży Pijarów, Warszawa

Kluk, K., 1808. Dykcyonarz roślinny, vol. II. Drukarnia Księży Pijarów, Warszawa

Kluk, K., 1811. Dykcyonarz roślinny, vol. III. Drukarnia Księży Pijarów, Warszawa

Kłusek, M., Kneisel, J., 2021. Woodland Management Practices in Bronze Age, Bruszczewo, Poland. Forests 12(10), 1327. https://doi.org/10.3390/f12101327

Knörzer, K.H., 1967. Subfossile Pflanzenreste von bandkeramischen Fundstellen im Rheinland. Archaeo-Physika 2, 3–29.

Knörzer, K.H., 1996. Beitrag zur Geschichte der Grünlandvegetation am Niederrhein. Tuexenia 16, 627–636.

Kofel, D., Andreasen, M.H., Jensen, P.M., 2017. Preliminary analysis of plant macrofossils from an Early Iron Age structure in Kærbøl, Denmark, with special emphasis on segetal and ruderal weeds. Acta Palaeobotanica 57(1), 109–118. https://doi.org/10.1515/acpa-2017-0006

Kohler-Schneider, M., Caneppele, A., 2009. Late Neolithic agriculture in eastern Austria: archaeobotanical results from sites of the Baden and Jevišovice cultures (3600–2800 b.c.). Vegetation History and Archaeobotany 18, 61–74. https://doi.org/10.1007/s00334-007-0129-3

Kołaczek, P., Rzodkiewicz, M., Karpińska-Kołaczek, M., Hildebrandt-Radke, I., Gałka, M., Jaeger, M., Kneisel, J., Niebieszczański, J., 2025. The impact of Lusatian Urnfield and subsequent prehistoric cultures on lake and woodland ecosystems: insights from multi-proxy palaeoecological investigations at Bruszczewo, western Poland. Vegetation History and Archaeobotany 34, 415–437. https://doi.org/10.1007/s00334-024-01022-7

Kondracki, J., 2012. Geografia Regionalna Polski. Wydawnictwo Naukowe PWN. (in Polish)

Kowal, T., 1953. Klucz do oznaczania nasion rodzajów *Chenopodium* L. i *Atriplex* L. (A key for the determination of the seeds of the genera *Chenopodium* L. and *Atriplex* L.). Monographiae Botanicae 1, 87–163.

Körber-Grohne, U., 1991. Identification key for subfossil Gramineae fruits. (Probleme der Kustenforschung im sudliche Nordeegebiet 18). Lax, Hildesheim.

Körber-Grohne, U., Kokabi, M., Piening, U., Planck, D., 1983. Flora und Fauna im Ostkastell von Welzheim. Forschungen und Berichte zur Vor- und Frühgeschichte in Baden-Württemberg 14. Theiss, Stuttgart.

Kozáková, R., Bobek, P., Dreslerová, D., Abraham, V., Svobodová-Svitavská, H., 2021. The prehistory and early history of the Šumava Mountains (Czech Republic) as seen through anthropogenic pollen indicators and charcoal data. The Holocene 31(1), 145–159. https://doi.org/10.1177/0959683620961484

Kozłowska, A., 1931. Elementy genetyczne i pochodzenie flory stepowej Polski. Mémoires de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles. Série B: Sciences Naturelles 4, 1–110. (in Polish)

Kubiak-Martens, L., 1996. Evidence for possible use of plant foods in Palaeolithic and Mesolithic diet from the site of Całowanie in the central part of the Polish Plain. Vegetation History and Archaeobotany 5, 33–38. https://doi.org/10.1007/BF00189433

Kubiak-Martens, L., 2002. New evidence for the use of root foods in pre-agrarian subsistence recovered from the late Mesolithic site at Halsskov, Denmark. Vegetation History and Archaeobotany 11, 23–31. https://doi.org/10.1007/s003340200003

Kujawska, M., Łuczaj, Ł., Sosnowska, J., Klepacki, P., 2016. Rośliny w wierzeniach i zwyczajach ludowych. Słownik Adama Fischera, Polskie Towarzystwo Ludoznawcze, Wrocław. (in Polish)

Kulik, M., Bochniak, A., Chabuz, W., Żółkiewski, P., Rysiak, A., 2023. Is Grazing Good for Wet Meadows? Vegetation Changes Caused by White-Backed Cattle. Agriculture 13(2), 261. https://doi.org/10.3390/agriculture13020261

Kuneš, P., Svobodová-Svitavská, H., Kolár, J., Hajnalová, J., Abraham, V., Macek, M., Tkác, P., Szabo, P., 2015. The origin of grasslands in the temperate forest zone of east central Europe: long-term legacy of climate and human impact. Quaternary Science Reviews 116, 15–27. https://doi.org/10.1016/j.quascirev.2015.03.014

Kunicka, D., 2012 (unpubl.). Analiza archeobotaniczna zawartości naczyń ze stanowiska kultury łużyckiej w Grodnie, gm. Chełmża. Praca magisterska. Uniwersytet Gdański.

Küster, H., 1988: Urnenfelderzeitliche Pflanzenreste aus Burkheim, Gemeinde Vogtsburg, Kreis Breisgau-Hochschwarzwald (Baden-Württemberg). In: Küster, H. (ed.), Der prähistorische Mensch und seine Umwelt. Festschrift für Udelgard Körber-Grohne. Forschungen und Berichte zur Vor- und Frühgeschichte in Baden-Württemberg 31. Stuttgart, pp. 261–268.

Kwiatkowska, A.J., Wyszomirski, T., 1988. Decline of *Potentillo albae-Quercetum* phytocoenoses associated with the invasion of *Carpinus betulus*. Vegetatio 75, 49–55. https://doi.org/10.1007/BF00044625

Ladouceur, E., Bonomi, C., Bruelheide, H., Klimešová, J., Burrascano, S., Poschlod, P., Tudela-Isanta, M., Iannetta, P., Mondoni, A., Amiaud, B., Cerabolini, B.E.L., Cornelissen, J.H.C., Craine, J., Louault, F., Minden, V., Öllerer, K., Onipchenko, V., Soudzilovskaia, N.A., Jiménez-Alfaro, B., 2019. The functional trait spectrum of European temperate grasslands. Journal of Vegetable Science 30(5), 777–788. https://doi.org/10.1111/jvs.12784

Lasota-Moskalewska, A., 1991. Hodowla i łowiectwo w Biskupinie na tle innych osiedli obronnych kultury łużyckiej (summary: Animal Breeding and Hunting at Biskupin Compared with Other Lusatian Culture Fortified Settlements). In: Jaskanis, J. (ed.), Prahistoryczny gród w Biskupinie. Problematyka osiedli obronnych na początku epoki żelaza, Warszawa, pp. 185–196.

Latałowa, M., 1976. Diagram pyłkowy osadów późnoglacjalnych i holoceńskich z torfowiska w Wolbromiu. Acta Palaeobotanica 17(1), 55–80.

Latałowa, M., 1982. Postglacial vegetational changes in the eastern Baltic coastal zone of Poland. Acta Palaeobotanica 22(2), 179–249.

Latałowa, M., 1992. Man and vegetation in the pollen diagrams from Wolin Island (NW Poland). Acta Palaeobotanica 32(1), 123–249.

Latałowa, M., 1999. Palaeoecological reconstruction of the environmental conditions and economy in early medieval Wolin – against a background of the Holocene history of the landscape. Acta Palaeobotanica 39(2), 183–271.

Latałowa, M., Nalepka, D., 1987. A study of the Late-Glacial and Holocene vegetational history of the Wolbrom area (Silesian-Cracovian Upland – S. Poland). Acta Palaeobotanica 27(1), 75–115.

Latałowa, M., Pińska, K., 2010. Zawartość botaniczna dwóch naczyń z pozostałości osady ludności łużyckich pól popielnicowych w Polanowie na Pojezierzu Gnieźnieńskim (summary: The botanical content of two vessels from the Lusatian Urnfield Culture site in Polanowo, the Gniezno Lake District). In: Pydyn, A. (ed.), Archeologia Jeziora Powidzkiego. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 197–226.

Latałowa, M., Badura, M., Jarosińska, J., 2003. Archaeobotanical samples from non-specific urban contexts as a tool for reconstructing environmental conditions (examples from Elbląg and Kołobrzeg, northern Poland). Vegetation History and Archaeobotany 12, 93–104. https://doi.org/10.1007/s00334-003-0011-x

Latałowa, M., Pędziszewska, A., Maciejewska, E., Święta-Musznicka J., 2013. *Tilia* forest dynamics, Kretzschmaria deusta attack, and mire hydrology as palaeoecological proxies for mid-Holocene climate reconstruction in the Kashubian Lake

District (N Poland). Holocene 23(5), 667–677. https://doi.org/10.1177/0959683612467484

Lehmair, T.A., Poschlod, P., Reisch, C., 2022. The impact of environment on genetic and epigenetic variation in *Trifolium pretense* populations from two contrasting semi-natural grasslands. Royal Society Open Science 9(5), 211406. https://doi.org/10.1098/rsos.211406

Lengyel, A., Swacha, G., Botta-Dukát, Z., Kącki, Z., 2020. Trait-based numerical classification of mesic, and wet grasslands in Poland. Journal of Vegetation Science 31, 319–330. https://doi.org/10.1111/jvs.12850

Lepówna, B., 1981. Materialne przejawy wierzeń ludności Gdańska w X–XIII wieku. Pomorania Antiqua 10, 169–198.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data using CANOCO. Cambridge. Cambridge University Press. https://doi.org/10.1017/CBO9780511615146

Lityńska-Zając, M., Wasylikowa, K., 2005. Przewodnik do badań archeobotanicznych (summary: Guidebook to archaeobotanical studies). Wydawnictwo Sorus. Poznań.

Lityńska-Zając, M., 2005. Chwasty w uprawach roślinnych w pradziejach i wczesnym średniowieczu (summary: Segetal weeds in prehistoric and early medieval farming). Wydawnictwo Instytutu Archeologii i Etnologii Polskiej Akademii Nauk, Kraków.

Lodwick, L., 2015. Identifying Ritual Deposition of Plant Remains: A Case Study of Stone Pine Cones in Roman Britain. In: Brindle, T., Allen, M., Durham, E., Smith, A. (eds), TRAC 2014, Oxbow Books, pp. 54–69. https://doi.org/10.2307/j.ctvh1dw2c.8

Lodwick, L.A., 2017. Agricultural innovations at a late Iron Age oppidum: archaeobotanical evidence for flax, food and fodder from calleva atrebatum, UK. Quaternary International 460, 198–219. https://doi.org/10.1016/j.quaint.2016.02.058

Ložek, V., 1973. Přiroda ve čtvrtohorach. Praha, Academia. (in Czech)

Łuczaj, Ł., Szymański, W.M., 2007. Wild vascular plants gathered for consumption in the Polish countryside: a review. Journal of Ethnobiology and Ethnomedicine 3, 17. https://doi.org/10.1186/1746-4269-3-17

Maciejewska, K., Badura, M., Noryśkiewicz, A.M., 2022. Botanical composition of meadows and pastures and their role in the functioning of early medieval semi-artificial lake islands in Ziemia Lubuska (Lubusz land), western Poland. Vegetation History and Archaeobotany 31, 579–594. https://doi.org/10.1007/s00334-022-00877-y

Madgwick, R., Esposito, C., Lamb, A.L., 2023. Farming and feasting during the Bronze Age–Iron Age transition in Britain (ca. 900–500 bce): multi-isotope evidence for societal change. Frontiers in Environmental Archaeology 2, 1221581. https://doi.org/10.3389/fearc.2023.1221581

Magyari, E.K., Chapman, J.C., Passmore, D.G., Allen, J.R.M., Huntley, J.P., Huntley, B., 2010. Holocene persistence of wooded steppe in the Great Hungarian Plain. Journal of Biogeography 37, 915–935. https://doi.org/10.1111/j.1365-2699.2009.02261.x

Makohonienko, M., 2000. Przyrodnicza historia Gniezna. Prace Zakładu Biogeografii i Paleoekologii UAM, 1. Homini, Poznań–Bydgoszcz. (in Polish)

Maltby, E., Acreman, M.C., 2011. Ecosystem services of wetlands: pathfinder for a new paradigm, Hydrological Sciences Journal 56(8), 1341–1359. https://doi.org/10.1080/02626667.2011.631014

Marek, S., 1954. Cechy morfologiczne i anatomiczne owoców rodzajów *Polygonum* L. i *Rumex* L. oraz klucze do ich oznaczania (Morphological and anatomical features of the fruits of genera *Polygonum* L., *Rumex* L. and keys for their determination). Monographiae Botanicae 2, 77–161.

Martin-Puertas, C., Matthes, K., Brauer, A., Muscheler, R., Hansen, F., Petrick, C., Aldahan, A., Possnert, G., Van Geel, B., 2012. Regional atmospheric circulation shifts induced by a grand solar minimum. Nature Geoscience Letters 5, 397–401. https://doi.org/10.1038/ngeo1460

Matuszkiewicz, J.M., 2008. Potential natural vegetation of Poland (Potencjalna roślinność naturalna Polski), IGiPZ PAN, Warszawa. Available from: https://www.igipz.pan.pl/Roslinnosc-potencjalna-zgik.html. Accessed September 2023.

Matuszkiewicz, W., 2001. Przewodnik do oznaczania zbiorowisk roślinnych. Państwowe Wydawnictwo Naukowe. (in Polish)

McCarty, M.M., Egri, M., Rustoiu, A., 2019. The archaeology of ancient cult: from foundation deposits to religion in Roman Mithraism. Journal of Roman Archaeology 32, 279–312. https://doi.org/10.1017/S1047759419000151

Menard, C., Duncan, P., Fleurance, G., Georges, J.-Y., Lila, M., 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. Journal of Applied Ecology 39, 120–133. https://doi.org/10.1046/j.1365-2664.2002.00693.x

Middleton, B.A., Holsten, B., Van Diggelen, R., 2006. Biodiversity management of fens and fen meadows by grazing, cutting and burning. Applied Vegetation Science 9(1), 307–316. https://doi.org/10.1111/j.1654-109X.2006.tb00680.x

Milberg, P., Fogelfors, H., Westerberg, L., Tälle, M., 2018. Annual burning of semi-natural grasslands for conservation: winners and losers among plant species. Nordic Journal of Botany 36(5), njb-01709. https://doi.org/10.1111/njb.01709

Milecka, K., 1998. Historia działalności człowieka w okolicach Giecza i Wagowa na podstawie analizy pyłkowej (summary: History of human activity in Giecz and Wagowo areas based on pollen analysis). In: Tobolski, K. (ed.), Biblioteka Studiów Lednickich III: 43–95.

Miotk-Szpiganowicz, G., Tobolski, K., Zachowicz, J., Nalepka, D., 2004. *Filipendula* Mill. – *Filipendula*. In: Ralska-Jasiewiczowa, M., Latałowa, M., Wasylikowa, K., Tobolski, K., Madeyska, E., Wright Jr., H.E., Turner, Ch. (eds), Late Glacial and Holocene history of vegetation in Poland based on isopollen maps, W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp. 297–304.

Mirek, Z., Piękoś-Mirkowa, H., Zając, A., Zając, M., 2020. Vascular Plants of Poland. An annotated checklist (Rośliny naczyniowe Polski. Adnotowany wykaz gatunków). W. Szafer Institute of Botany, Polish Academy of Sciences.

Moldenhawer, K., 1948. Główniejsze zboża występujące w wykopaliskach Biskupina (Wielkopolskiego) (summary: The principal cereals in the Biskupin findings of the Early Iron-Age). Roczniki Nauk Rolniczych 51, 306–312.

Moog, D., Poschlod, P., Kahmen, S., Schreiber, K.F., 2002. Comparison of species composition between different grassland management treatments after 25 years. Applied Vegetation Science 5(1), 99–106. https://doi.org/10.1111/j.1654-109X.2002.tb00539.x

Moskal-del Hoyo, M., 2021. Open canopy forests of the loess regions of southern Poland: a review based on wood charcoal assemblages from Neolithic and Bronze Age archaeological sites. Quaternary International 593–594, 204–223. https://doi.org/10.1016/j.quaint.2020.11.013

Moskal-del Hoyo, M., Mueller-Bieniek, A., Alexandrowicz, W.P., Wilczyński, J., Wędzicha, S., Kapcia, M., Przybyła, M.M., 2017. The continuous persistence of open oak forests in the Miechów Upland (Poland) in the second half of the Holocene. Quaternary International 458, 14–27. https://doi.org/10.1016/j.quaint.2016.11.017

Moskal-del Hoyo, M., Wacnik, A., Alexandrowicz, W.P., Stachowicz-Rybka, R., Wilczyński, J., Pospuła-Wędzicha, S., Szwarczewski, P., Korczyńska, M., Cappenberg, K., Nowak, M., 2018. Open country species persisted in loess regions during the Atlantic and early Subboreal phases: New multidisciplinary data from southern Poland. Review of Palaeobotany and Palynology 253, 49–69. https://doi.org/10.1016/j.revpalbo.2018.03.005

Moskal-del Hoyo, M., Lityńska-Zając, M., Juźwińska, G., Kruk, J., Oberc, T., Włodarczak, P., 2025. Use of woodland plant resources at the Neolithic site at Bronocice (southern Poland). Journal of Archaeological Science: Reports 61, 104943. https://doi.org/10.1016/j.jasrep.2024.104943

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., García, R.G., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M., Tichý, L., 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19, 3–264. https://doi.org/10.1111/avsc.12257

Mueller-Bieniek, A., Nalepka, D., 2010. Czy znaleziska ostnicy (*Stipa* sp.) z neolitu południowych Kujaw świadczą o istnieniu muraw kserotermicznych w optimum klimatycznym? (abstract: Do findings of feather grass (*Stipa* sp.) from the Neolithic of Southern Kujawy region indicate the existence of xerothermic grasslands during the climatic optimum?). In: Ratyńska, H., Waldon B. (eds), Ciepłolubne murawy w Polsce – stan zachowania i perspektywy ochrony. Uniwersytet Kazimierza Wielkiego, Bydgoszcz, pp. 235–248.

Mueller-Bieniek, A., Pyzel, J., Kapcia, M., 2018. *Chenopodium* seeds in open-air archaeological sites – how to not throw the baby out with the bathwater. Environmental Archaeology 25(1), 69–81. https://doi.org/10.1080/14614103.2018.1536500

Mueller-Bieniek, A., Bogucki, P., Pyzel, J., Kapcia, M., Moskal-del Hoyo, M., Nalepka, D., 2019. The role of *Chenopodium* in the subsistence economy of pioneer agriculturalists on the northern frontier of the Linear Pottery culture in Kuyavia, central Poland. Journal of Archaeological Science 111, 105027. https://doi.org/10.1016/j.jas.2019.105027

Németh, A., Bárány, A., Csorba, G., Magyari, E., Pazonyi, P., Pálfy, J., 2017. Holocene mammal extinctions in the Carpathian Basin: a review. Mammal Review 47, 38–52. https://doi.org/10.1111/mam.12075

Nielsen, A.B., Giesecke, T., Theuerkauf, M., Feeser, I., Behre, K-E., Beug, H-J., Chen, S-H., Christiansen, J., Dörfler, W., Endtmann, E., Jahns, S., de Klerk, P., Kühl, N., Latałowa, M., Odgaard, B.V., Rasmussen, P., Stockholm, J.R., Voigt, R., Wiethold, J., Wolters, S., 2012. Quantitative reconstructions of changes in regional openness in north-central Europe reveal new insights into old questions. Quaternary Science Reviews 47, 131–149. https://doi.org/10.1016/j.quascirev.2012.05.011

Nielsen, N.H., Kristiansen, S.M., Ljungberg, T., Enevold, R., Løvschal, M., 2019. Low and variable: Manuring intensity in Danish Celtic fields. Journal of Archaeological Science Reports 27, 101955. https://doi.org/10.1016/j.jasrep.2019.101955

Nielsen, N.H., Henriksen, P.S., Mortensen, M.F., Enevold, R., Mortensen, M.N., Scavenius, C., Enghild, J.J., 2021. The last meal of Tollund Man: new analyses of his gut content. Antiquity 95(383), 1195–1212. https://doi.org/10.15184/aqy.2021.98

Nießen, I., 2017. Building sacrifices and magical protection: a study in canton of Grisons (CH). In: Bis-Worch C., Theune, C. (eds), Religion, Cults and Rituals in the medieval rural environment, Ruralia 11, pp. 325–336. https://doi.org/10.59641/oet917hq

Niewiarowski, W., Kot, R., 2010. Delimitacja i charakterystyka gatunków i odmian krajobrazu naturalnego Pojezierza Chełmińsko-Dobrzyńskiego, Równiny Urszulewskiej oraz przyległych dolin Wisły i Drwęcy. Przegląd Geograficzny 82(3), 335–365. https://doi.org/10.7163/PrzG.2010.3.2

Niewiarowski, W., Noryśkiewicz, B., 1999. Environmental changes in the vicinity of Biskupin in selected periods of the last six thousand years and their reflection in pollen diagrams. Acta Palaeobotanica, Suppl. 2, 581–588.

Niezabitowski, E., 1938. Szczątki zwierzęce i ludzkie osady przedhistorycznej w Biskupinie (summary: Les restes d'animaux trouvés dans la station préhistorique de Biskupin). Przegląd Archeologiczny 5(2), 92–103.

Noryśkiewicz, A.M., 2013. Historia roślinności i osadnictwa ziemi chełmińskiej w późnym holocenie. Studium palinologiczne (summary: Vegetation and settlement history of the Chełmno Land in late Holocene. Palynological study). Toruń. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika.

Nowak, B., 2019. Położenie Jeziora Powidzkiego. In: Nowak, B. (ed.), Jezioro Powidzkie wczoraj i dziś. Instytut Meteorologii i Gospodarki Wodnej – Państwowy Instytut Badawczy, Warszawa, pp. 9–13.

Nowak, B., Jawgiel, K., Nadolna, A., 2019a. Morfometria Jeziora Powidzkiego. In: Nowak, B. (ed.), Jezioro Powidzkie wczoraj i dziś. Instytut Meteorologii i Gospodarki Wodnej – Państwowy Instytut Badawczy, Warszawa, pp. 31–36.

Nowak, B., Nadolna, A., Kowalewski, G., 2019b. Przemiany hydrograficzne jeziora Powidzkiego i jego okolic. In: Nowak, B. (ed.), Jezioro Powidzkie wczoraj i dziś. Instytut Meteorologii i Gospodarki Wodnej – Państwowy Instytut Badawczy, Warszawa, pp. 21–29.

Öllerer, K., Varga, A., Kirby, K., Demeter, L., Biró, M., Bölöni, J., Molnár, Z., 2019. Beyond the obvious impact of domestic livestock grazing on temperate forest vegetation – A global review. Biological Conservation 237, 209–2019. https://doi.org/10.1016/j.biocon.2019.07.007

Orlicka-Jasnoch, J., 2019. Skarb ludności kultury łużyckiej z Nowego Kramska. Aspekt archeologiczny (summary: The hoard of the Lusatian culture people from Nowe Kramsko. Archaeaological aspect). In: Michalak, A., Orlicka-Jasnoch, J. (eds), Skarb z Nowego Kramska. Analizy. Konteksty. Muzeum Archeologiczne Środkowego Nadodrza w Zielonej Górze, Zielona Góra, pp. 17–138.

Ozinga, W.A., Colles, A., Bartish, I.V., Hennion, F., Hennekens, S.M., Pavoine, S., Poschlod, P., Hermant, M., Schaminée, J.H.J., Prinzing, A., 2013. Scarce descendants of specialists. Global Ecology and Biogeography 22(2), 213–222. https://doi.org/10.1111/j.1466-8238.2012.00792.x

Pagel, E., Poschlod, P., Reisch, C., 2020. Habitat matters – Strong genetic and epigenetic differentiation in *Linum catharticum* from dry and wet grasslands. Ecology and Evolution 10, 10271–10280. https://doi.org/10.1002/ece3.6689

Palmer, C., 2004. Palaeoeconomic and palaeoenvironmental studies: 1. The carbonized macroscopic plant remains. In: Harding, A., Ostoja-Zagórski, J., Palmer, C., Rackham, J. (eds), Sobiejuchy. A Fortified Site of the Early Iron Age in Poland. Institute of Archaeology and Ethnology Polish Academy of Sciences, Warsaw, pp. 66–86.

PAP – Science and Scholarship in Poland 2017. Sour soup for the gods – discovery in a medieval hut in the Lublin province. Available from: https://scienceinpoland.pl/en/news/news,414240,sour-soup-for-the-gods---discovery-in-a-medieval-hut-in-the-lublin-province.html#copyrightsText. Accessed June 2025.

Park, J., Park, J., Yi, S., Kim, J.C., Lee, E., Choi, J., 2019. Abrupt Holocene climate shifts in coastal East Asia, including the 8.2 ka, 4.2 ka, and 2.8 ka BP events, and societal responses on the Korean peninsula. Scientific Reports 9, 10806. https://doi.org/10.1038/s41598-019-47264-8

Pärtel, M., Bruun, H.H., Sammul, M., 2005. Biodiversity in temperate European grasslands: origin and conservation. Grassland Science in Europe 10, 1–14.

Paul, W., 2012. Xerothermic species of the genus *Campanula* in Poland – a model for the phylogeographical assessment of reconstruction of post-glacial migration routes. Annales Universitatis Mariae Curie-Skłodowska 67(1), 27–36.

Paulsson-Holmberg, T., 1998. Iron Age building offerings. A contribution to the analysis of a die-hard phenomenon in Swedish preindustrial agrarian society. Fornvännen 92(3/4), 163–175.

Pędziszewska, A., Latałowa, M., 2016. Stand-scale reconstruction of late Holocene forest succession in the Gdańsk Upland (northern Poland) based on integrated palynological and macrofossil data from paired sites. Vegetation History and Archaeobotany 25, 239–254. https://doi.org/10.1007/s00334-015-0546-7

Pędziszewska, A., Latałowa, M., Święta-Musznicka, J., Zimny, M., Kupryjanowicz, M., Noryśkiewicz, A.M., Bloom, K., 2020. Pollen Evidence of Change in Environment and Settlement during the 1st Millennium A.D. In: Bursche, A., Hines, J., Zapolska, A. (eds), The Migration Period between the Oder and the Vistula. Vol. 1, Koninklijke Brill NV, Leiden, The Netherlands, pp. 137–198. https://doi.org/10.1163/9789004422421_006

Piątkowska-Małecka, J., 1999. Konsumpcja mięsa w Grodnie – osadzie z wczesnej epoki żelaza. Światowit 1(42) Fasc. B, 178–185. (in Polish)

Pińska, K., Latałowa, M., 2014. Plant remains. In: Chudziak, W., Kaźmierczak, R. (eds), The Island in Żółte on Lake Zarańskie. Early Medieval Gateway into West Pomerania. Institute of Archaeology. Nicolaus Copernicus University, Toruń, pp. 367–419.

Pleskot, K., Tjallingii, R., Makohonienko, M., Nowaczyk, N., Szczuciński, W., 2018. Holocene paleohydrological reconstruction of Lake Strzeszyńskie (western Poland) and its implications for the central European climatic transition zone. Journal of Paleolimnology 59, 443–459. https://doi.org/10.1007/s10933-017-9999-2

Pokorná, A., Kočár, P., Novák, J., Šálková, T., Žáčková, P., Komárková, V., Vaněček, Z., Sádlo, J., 2018. Ancient and Early Medieval man-made habitats in the Czech Republic: colonization history and vegetation changes. Preslia 90, 171–193. https://doi.org/10.23855/preslia.2018.171

Pokorný, P., Chytrý, M., Juřičková, L., Sádlo, J., Novák, J., Ložek, V., 2015. Mid-Holocene bottleneck for central European dry grasslands: Did steppe survive the forest optimum in northern Bohemia, Czech Republic? The Holocene 25(4), 716–726. https://doi.org/10.1177/0959683614566218

Polcyn, M., 1995. Plant remains in a Early Medieval pot from Ostrów Lednicki. In: Kroll, H., Pasternak, R. (eds), Res archaeobotanicae. International workgroup for palaeoethnobotany. Proceedings of the nineth Symposium Kiel 1992, pp. 249–259.

Poschlod, P., 2015. The Origin and Development of the Central European Man-made Landscape, Habitat and Species Diversity as Affected by Climate and its Changes – a Review. Interdisciplinaria Archaeologica 6(2), 197–221. https://doi.org/10.24916/iansa.2015.2.5

Poschlod, P., Bakker, J.P., Kahmen, S., 2005. Changing land use and its impact on biodiversity. Basic and Applied Ecology 6(2), 93–98. https://doi.org/10.1016/j.baae.2004.12.001

Poschlod, P., Baumann A., Karlik, P., 2009. Origin and development of grasslands in central Europe. In: Veen, P., Jefferson, R., De Smidt, J., Van der Straaten, J. (eds), Grasslands in Europe – of high nature value. Koninklijke Nederlandse Natuurhistorische Vereniging Publishing, Zeist, pp. 15–25. https://doi.org/10.1163/9789004278103_003

Prajs, B., Rogalski, M., Sotek, Z., Stasińska, M., 2010. Xerothermic Grassland Communities of the Alliance *Cirsio-Brachypodion pinnati* Hadac et Klika 1944 em. Krausch 1961 in Northwestern Poland. Polish Journal of Environmental Studies 19(1), 141–148.

Pydyn, A., Rembisz, A., 2010. Osadnictwo ludności łużyckich pól popielnicowych w strefie brzegowej Jeziora Powidzkiego (abstract: Settlements of the Lusatian Urnfield Culture communities in the area of Lake Powidz). In: Pydyn, A. (ed.), Archeologia Jeziora Powidzkiego. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 99–130.

Pydyn, A., 2010. Archeologiczne penetracje podwodne Jeziora Powidzkiego (summary: Underwater archaeological survey of the coastal zone of Lake Powidz) In: Pydyn, A. (ed.), Archeologia Jeziora Powidzkiego. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 15–40.

Pykälä, J., 2000, Mitigating Human Effects on European Biodiversity through Traditional Animal Husbandry. Conservation Biology 14(3), 705–712. https://doi.org/10.1046/j.1523-1739.2000.99119.x

Raduła, M.W., Szymura, T.H., Szymura, M., Swacha, G., 2022. Macroecological drivers of vascular plant species composition in semi-natural grasslands: A regional study from Lower Silesia (Poland). Science of the Total Environment 833, 155151. https://doi.org/10.1016/j.scitotenv.2022.155151

Ralska-Jasiewiczowa, M., Demske, D., Van Geel B., 1998. Late-Glacial vegetation history recorded in the Lake Gościąż sediments. In: Ralska-Jasiewiczowa, M., Goslar, T., Madeyska, T., Starkel, L. (eds). Lake Gościąż, Central Poland. A Monographic Study. Part 1, W. Szafer Institute of Botany. Polish Academy of Sciences, Kraków, pp. 128–143.

Ralska-Jasiewiczowa, M., Latałowa, M., Wasylikowa, K., Tobolski, K., Madeyska, E., Wright Jr., H.E., Turner, Ch. (eds), 2004. Late Glacial and Holocene History of Vegetation in Poland based on Isopollen Maps. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Ralska-Jasiewiczowa, M., Van Geel, B., 1998. Human impact on the vegetation of the Lake Gościąż surroundings in prehistoric and early-historic times. In: Ralska-Jasiewiczowa, M., Goslar, T., Madeyska, T., Starkel, L. (eds), Lake Gościąż, Central Poland. A Monographic Study. Part 1, W. Szafer Institute of Botany. Polish Academy of Sciences, Kraków, pp. 267–293.

Rasmussen, P., 1989. Leaf-foddering of livestock in the Neolithic: archaeobotanical evidence from Weier, Switzerland, Danish. Journal of Archaeology 8, 51–71. https://doi.org/10.1080/0108464X.1989.10590019

Rasmussen, P., 1993. Analysis of goat/sheep faeces from Egolzwil 3, Switzerland: Evidence for branch and twig foddering of livestock in the Neolithic. Journal of Archaeological Science 20, 479–502. https://doi.org/10.1006/jasc.1993.1030

Reed, K., 2024. Let me be fodder: Unravelling human and animal derived plant remains recorded from Roman Mursa, Croatia, Quaternary International 699, 23–34. https://doi.org/10.1016/j.quaint.2024.02.008

Rembisz, A., 2010. Przedmioty użytkowe z osady z wczesnej epoki żelaza w Polanowie pow. Słupca, woj. wielkopolskie, stanowisko 12 (z badań w latach 2004–2006) (abstract: Archaeological finds from the Early Iron Age settlement in Polanowo, Słupca district, wielkopolskie voivodeship, site 12 (from the excavation 2004–2006)). In: Pydyn, A. (ed.). Archeologia Jeziora Powidzkiego. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 77–98.

Rembisz, A., 2011. Osada ludności kultury łużyckiej w Rudzie gm. Grudziądz (stanowisko 3-6) na tle osadnictwa Kotliny Grudziądzkiej. PhD Thesis, Nicolaus Copernicus University, Institute of Archaeology, Toruń. (in Polish)

Rembisz, A., Gackowski, J., Makowiecki, D., Markiewicz, M., Polcyn, M., 2009. Ślady gospodarki roślinno-zwierzęcej ludności kultury łużyckich pól popielnicowych z osady w Rudzie, gmina Grudziądz, północna Polska (abstract: The evidence of plant cultivation and animal farming in the settlement of the Lusatian Urnfield Culture at Ruda, Grudziądz district (N Poland)). In: Domańska, L., Kittel, P., Forysiak, J. (eds), Środowiskowe uwarunkowania lokalizacji osadnictwa. Środowisko – Człowiek – Cywilizacja, tom 2. Seria wydawnicza Stowarzyszenia Archeologii Środowiskowej. Bogucki Wydawnictwo Naukowe, Poznań, pp. 109–122.

Reutimann, P., Billeter, R., Dengler, J., 2023. Effects of grazing versus mowing on the vegetation of wet grasslands in the northern Pre-Alps, Switzerland. Applied Vegetation Science 26, e12706. https://doi.org/10.1111/avsc.12706

Robin, V., Nelle, O., Talon, B., Poschlod, P., Schwartz, D., Bal, M.-C., Allée, P., Vernet, J.-L., Dutoit, T., 2018. A comparative review of soil charcoal data: Spatiotemporal patterns of origin and long-term dynamics of Western European nutrient-poor grasslands. The Holocene 28(8), 1313–1324. https://doi.org/10.1177/0959683618771496

Robinson, M., 1999. The macroscopic plant remains. In: Fulford, M., Wallace-Hadrill, A. (eds), Towards a history of pre-roman Pompeii: excavations beneath the House of Amarantus (I.9.11-12), 1995-8. Papers of the British School at Rome 67, 95–102, 139–144.

Robinson, M., 2002. Domestic burnt offerings and sacrifices at Roman and pre-Roman Pompeii, Italy. Vegetation History and Archaeobotany 11, 93–100. https://doi.org/10.1007/s003340200010

Roo-Zielińska, E., 2001. Gatunki charakterystyczne zbiorowisk łąkowych z klasy *Molinio-Arrhenatheretea* jako wskaźniki warunków siedliskowych (summary: Characteristic species of meadow communities representing *Molinio-Arrhenatheretea* class as indicators of the abiotic condtions). In: Roo-Zielińska, E., Solon, J. (eds), Typologia zbiorowisk i kartografia roślinności w Polsce – rozważania nad stanem współczesnym (Community typology and vegetational cartography in Poland – some thoughts on the current state of affairs), Prace Geograficzne 178, Polska Akademia Nauk, Instytut Geografii i Przestrzennego Zagospodarowania im. Stanisława Leszczyckiego Warszawa, pp. 231–260.

Roo-Zielińska, E., 2014. Wskaźniki ekologiczne zespołów roślinnych Polski (summary: Ecological indicators of plant associations in Poland). Polska Akademia Nauk, Instytut Geografii i Przestrzennego Zagospodarowania im. Stanisława Leszczyckiego, Sedno Wydawnictwo Akademickie.

Rovira, N., Chabal, L., 2008. A foundation offering at the Roman port of Lattara (Lattes, France): the plant remains. Vegetation History and Archaeobotany 17, 191–200. https://doi.org/10.1007/s00334-008-0174-6

Sady, A., 2015. Szczątki roślinne z osady w Grzybianach (summary: Plant remains from Grzybiany settlement). In: Stolarczyk, T., Baron, J. (eds), Osada kultury pól popielnicowych w Grzybianach koło Legnicy. Muzeum Miedzi w Legnicy, Legnica-Wrocław. pp. 431–475.

Šálková, T., Vobejda, L., Chvojka, O., Beneš, J., Vondrovský, V., Kuna, M., Křivánek, R., Menšík, P., Novák, J., 2022. Extensive archaeobotanical data estimate carrying capacity, duration, and land use of the Late Bronze Age settlement site Březnice (Czech Republic). Scientific Reports 12, 20323. https://doi.org/10.1038/s41598-022-24753-x

Schieltz, J.M., Rubenstein, D.I., 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know?. Environmental Research Letters 11, 113003. https://doi.org/10.1088/1748-9326/11/11/113003

Sienkiewicz–Paderewska, D., Paderewski, J., Suwara, I., Kwasowski, W., 2020. Fen grassland vegetation under different land uses (Biebrza National Park, Poland). Global Ecology and Conservation 23, e01188. https://doi.org/10.1016/j.gecco.2020.e01188

Söderström, B., Svensson, B., Vessby, K., Glimskär, A., 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiversity and Conservation 10, 1839–1863. https://doi.org/10.1023/A:1013153427422

Sonnier, G., Boughton, E.H.,Whittington, R., 2023. Long-Term Response of Wetland Plant Communities to Management Intensity, Grazing Abandonment, and Prescribed Fire. Ecological Applications 33(1), e2732. https://doi.org/10.1002/eap.2732

Speier, M., 1994. Vegetationskundliche und paläoökologische Untersuchungen zur Rekonstruktion prähistorischer und historischer Landnutzungen im südlichen Rothaargebirge. Abhandlungen aus dem Westfälischen Provinzial-Museum für Naturkunde 56(3/4), 3–174.

Stammel, B., Kiehl, K., Pfadenhauer, J., 2003. Alternative management on fens: Response of vegetation to grazing and mowing. Applied Vegetation Science 6, 245–254. https://doi.org/10.1111/j.1654-109X.2003.tb00585.x

Stokes, P., Rowley-Conwy, P., 2002. Iron Age Cultigen? Experimental Return Rates for Fat Hen (*Chenopodium album* L.). Environmental Archaeology 7, 95–99. https://doi.org/10.1179/env.2002.7.1.95

Sucholas, J., Molnár, Z., Łuczaj, Ł., Poschlod, P., 2022. Local traditional ecological knowledge about hay management practices in wetlands of the Biebrza Valley, Poland. Journal of Ethnobiology and Ethnomedicine 18, 9. https://doi.org/10.1186/s13002-022-00509-9

Swacha, G., Botta-Dukát, Z., Kącki, Z., Pruchniewicz, D., Żołnierz, L., 2018. The effect of abandonment on vegetation composition and soil properties in *Molinion* meadows (SW Poland). PLoS ONE 13(5), e0197363. https://doi.org/10.1371/journal.pone.0197363

Swacha, G., Meserszmit, M., Pavlů, L., Pavlů, V.V., Kajzrová, K., Kassahun, T., Raduła, M., Titěra, J., Kącki, Z., 2023. Drivers of species-specific contributions to the total live aboveground plant biomass in Central European semi-natural hay grasslands. Ecological Indicators 146, 109740. https://doi.org/10.1016/j.ecolind.2022.109740

Święta-Musznicka, J., Latałowa, M., Pryczkowska, M., 2010. Wyniki sondażowych analiz paleoekologicznych osadów strefy litoralnej Jeziora Powidzkiego na Pojezierzu Gnieźnieńskim (abstract: The result of sounding paleoecological examination of sediments in the littoral zone of Lake Powidz in the Gniezno Lake District). In: Pydyn, A. (ed.), Archeologia Jeziora Powidzkiego. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń, pp. 177–196.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2018. Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. Biodiversity and Conservation 27, 2451–2475. https://doi.org/10.1007/s10531-018-1562-6

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2016. Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. Agriculture, Ecosystems & Environment 222, 200–212. https://doi.org/10.1016/j.agee.2016.02.008

Tipping, R., Davies, A., McCulloch, R., Tisdall, E., 2008. Response to late Bronze Age climate change of farming communities in north east Scotland. Journal of Archaeological Science 35, 2379–2386. https://doi.org/10.1016/j.jas.2008.03.008

Tobolski, K., 1990. Paläoökologische Untersuchungen des Siedlungsgebietes im Lednica Landschaftspark (Nordwestpolen). Offa 47, 109–131.

Tomczyk, A., Szyga-Pluta, K., 2019. Variability of thermal and precipitation conditions in the growing season in Poland in the years 1966–2015. Theoretical and Applied Climatology 135, 1517–1530. https://doi.org/10.1007/s00704-018-2450-4

Tomczyk, A.M., Bednorz, E., Szyga-Pluta, K., 2021. Changes in Air Temperature and Snow Cover in Winter in Poland. Atmosphere 12(1), 68. https://doi.org/10.3390/atmos12010068

Turney, C.S.M., Jones, R.T., Thomas, Z.A., Palmer, J.G., Brown, D., 2016. Extreme wet conditions coincident with Bronze Age abandonment of upland areas in Britain. Anthropocene 13, 69–79. https://doi.org/10.1016/j.ancene.2016.02.002

Tylmann, W., Pędziszewska, A., Żarczyński, M., Latałowa, M., Zolitschka, B., 2024. Lake level fluctuations and varve preservation – The sediment record from Lake Suminko (Poland) reflects European paleoclimatic changes. Quaternary Science Reviews 339, 108854. https://doi.org/10.1016/j.quascirev.2024.108854

Urban, J., 2019. Gospodarka rolna społeczności tzw. kultury łużyckiej (summary in English). Wydawnictwo Instytutu Archeologii i Etnologii PAN. (in Polish)

Valkó, O., Venn, S., Żmihorski, M., Biurrun, I., Labadessa, R., Loos, J., 2018. The challenge of abandonment for the sustainable management of Palaearctic natural and semi-natural grasslands. Hacquetia 17(1), 5–16. https://doi.org/10.1515/hacq-2017-0018

Van Geel, B., Buurman, J., Waterbolk, H.T., 1996. Archaeological and palaeoecological indications of an abrupt climate change in The Netherlands, and evidence for climatological teleconnection around 2650 BP. Journal of Quaternary Science 11(6), 451–460. https://doi.org/10.1002/(SICI)1099-1417(199611/12)11:6<451::AID-JQS275>3.0.CO;2-9

Van Geel, B., Bokovenko, N.A., Burova, N.D., Chugunov, K.V., Dergachev, V.A., Dirksen, V.G., Kulkova, M., Nagler, A., Parzinger, H., Van der Plicht, J., Vasiliev, S.S., Zaitseva, G.I., 2004. Climate change and the expansion of the Scythian culture after 850 BC: a hypothesis. Journal of Archaeological Science 31(12), 1735–1742. https://doi.org/10.1016/j.jas.2004.05.004

Van Zeist, W., 1991. Economic aspects. In: Van Zeist, W., Wasylikowa, K., Behre, K.-E. (eds), Progress in Old World Palaeoethnobotany. Rotterdam, Balkema, pp. 109–130.

Vera, F.W.M., 2000. Grazing ecology and forest history. CABI publishing.

Vinogradova, O., Gaillard, M.-J., Andrén, E., Palm, V., Rönnby, J., Dahl, M., Almgren, E., Karlsson, J., Nielsen, A.B., Åkesson, C., Andrén, T., 2023. 3000 Years of past regional and local land-use and land-cover change in the southeastern Swedish coastal area: Early human-induced increases in landscape openness as a potential nutrient source to the Baltic Sea coastal waters. The Holocene 34(1), 56–73. https://doi.org/10.1177/09596836231200433

Wanner, H., Solomina, O., Grosjean, M., Ritz, S.P., Jetel, M., 2011. Structure and origin of Holocene cold events. Quaternary Science Reviews 30(21–22), 3109–3123. https://doi.org/10.1016/j.quascirev.2011.07. 010

Ważny, T., 2009. Dendrochronologia drewna biskupińskiego, czyli co drzewa zapisały w przyrostach rocznych (summary: Dendrochronology of the Biskupin timbers, or, what the tree-rings of Biskupin have to say). In: Babiński, L. (ed.), Stan i perspektywy zachowania drewna biskupińskiego. Muzeum Archeologiczne w Biskupinie, Biskupin, pp. 63–76.

Ważny, T., 2010. Skład gatunkowy drewna użytego do budowy osad ludności łużyckich pól popielnicowych w Powidzu i Polanowie na pojezierzu Gnieźnieńskim (abstract: Wood's species used to construct the Lusatian Urnfield Culture settlements in Powidz and Polanowo in the Gniezno Lake District). In: Pydyn, A. (ed.), Archeologia Jeziora Powidzkiego, pp. 239–246.

Willerding, U., 1991. Präsenz, Erhaltung und Repräsentanz von Pflanzenresten in archäologischem Fundgut. In: Van Zeist, W., Wasylikowa, K., Behre, K-E. (eds), Progress in Old World Palaeoethnobotany. A.A. Balkema, Rotterdam-Brookfield, pp. 25–51.

Willner, W., Moser, D., Plenk, K., Aćić, S., Demina, O.N., Höhn, M., Kuzemko, A., Roleček, J., Vassilev, K., Vynokurov, D., Kropf, M., 2021. Long-term continuity of steppe grasslands in eastern Central Europe: Evidence from species distribution patterns and chloroplast haplotypes. Journal of Biogeography 48(12), 3104–3117. https://doi.org/10.1111/jbi.14269

Willner, W., Roleček, J., Korolyuk, A., Dengler, J., Chytrý, M., Janišová, M., Lengyel, A., Aćić, S., Becker, T., Ćuk, M., Demina, O., Jandt, U., Kącki, Z., Kuzemko, A., Kropf, M., Lebedeva, M., Semenishchenkov, Y., Šilc, U., Stančić, Z., Staudinger, M., Vassilev, K., Yamalov, S., 2019. Formalized classification of semi-dry grasslands in central and eastern Europe. Preslia 91, 25–49.

Woodbridge, J., Fyfe, R.M., Roberts, N., Downey, S., Edinborough, K., Shennan, S., 2014. The impact of the Neolithic agricultural transition in Britain: a comparison of pollen-based land-cover and archaeological 14C date-inferred population change. Journal of Archaeological Science 51, 216–224. https://doi.org/10.1016/j.jas.2012.10.025

Zanon, M., Davis, B.A.S., Marquer, L., Brewer, S., Kaplan, J.O., 2018. European Forest Cover During the Past 12,000 Years: A Palynological Reconstruction Based on Modern Analogs and Remote Sensing. Frontiers in Plant Science 9, 253. https://doi.org/10.3389/fpls.2018.00253

Zarzycki, K., Trzcińska-Tacik, H., Różański, W., Szeląg, Z., Wołek, J., Korzeniak, U., 2002. Ecological indicator values of vascular plants of Poland (Ekologiczne liczby wskaźnikowe roślin naczyniowych Polski). Biodiversity of Poland (Różnorodność Biologiczna Polski), Vol. 2. W. Szafer Institute of Botany. Polish Academy of Sciences. Kraków.