Since domesticated plants moved from moderate Mediterranean climates in south-west Asia where their domestication took place to different latitudes and altitudes, these species have had to endure both genetic and morphotypical changes. Upon reaching the East Baltic, crops like wheat and barley were exposed to a different environment consisting of a continental climate with very distinct seasonal patterns, different soils, vernalization and photoperiod patterns that were crucial for plant development and growth. In this paper I take previously postulated ideas on the delay of agriculture in north-west Europe and the Alpine region of Eurasia to suggest that similar reasons could have been responsible for the delay of cereal cultivation in the eastern Baltic region.

Here I argue that the slow introduction rate of cereal cultivation occurred not only due to human choice, as alternative wild resources were available, but due to the time it took for crops to adjust to environmental changes. In addition, the establishment of an ultimate crop species package was an important development that allowed better plant adaptation to novel environmental conditions and the reduction of crop failure.

In this publication the term “geographical margin” is used not in the sense of climatic hostility and difficulties for human subsistence but rather from the perspective of plant species of south-west Asian origin.

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Introduction

Since the earliest domestication in south-west Asia (East Turkey, Levant) around the 9th millennium BC (Fuller et al. 2011; Zohary et al. 2012) crops have spread across the world to different latitudes and altitudes. The initial spread of agriculture across Europe took place along two principal routes, one following the loess belt through Central and East Europe as the LBK culture, and the second wave of agriculture following a route along the Mediterranean coast as the Cardial Pottery Culture (Price 2000; Milisauskas 2011). In some regions agriculture was adopted very quickly, while conversely it took thousands of years for domesticated
crops to be adapted in the East Baltic. According to Diamond (2002), the fastest dispersal of plants and animals happened along the same latitudes. For example, from initial domestication to the 8th millennium BC, plants spread to the Mediterranean zone of west Anatolia and the southern Balkans (Perlès 2001), while in north-east Europe we see the earliest evidence of agriculture only during the middle of the 2nd millennium BC (Grikpėdis & Motuzaite Matuzeviciute 2017). The pace of spread of agriculture across Europe was also slower in the Alpine regions (Jones et al. 2012) and the North European Plain (Zvelebil & Rowley-Conwy 1991; Zvelebil & Lillie 2000). In Scandinavia early agriculture first expanded to the southern region (Sørensen & Karg 2014) where the climate is fairly mild when compared to most other regions of the world of similar northern latitudes (Climate Map of Sweden 2018). The spread to the northern part of Scandinavia, however, away from the Gulf Steam-influenced areas, took much longer. The cause of such variations in the pace of agricultural spread has been a topic of debate among archaeologists. For the eastern Baltic region, it has been explained as a local hunter-gatherer choice to stick to the abundantly available wild resources (Zvelebil & Rowley-Conwy 1984; Zvelebil 1995; Janik 2011; Grikpėdis & Motuzaite Matuzeviciute 2017).

While talking about agricultural dispersal researchers tend to think about this phenomenon mainly from human perspectives and its adoption via demic or cultural diffusion (Zvelebil 1996). While this is the case in some areas, we rarely consider the spread of agriculture from the perspectives of the plant species themselves. There are clear climatic constraints on why grapes or figs cannot grow or do poorly in northern latitudes. Therefore, it is not surprising that the domesticated south-west Asian grasses had also encountered a variety of environmental constraints in northern latitudes during their initial phase of dispersal. Previous research has shown that Neolithic crops in northern Europe (Scandinavia) were smaller due to environmental stress (Fuller et al. 2017). The Chinese millets, which tolerate hot and dry climates, had also encountered ecological constraints on the way from China to Europe. During prehistoric times Chinese millets were cultivated only as far north as Latvia, while in Scandinavia and the British Isles they were virtually absent.

Plants need to undergo special genetic adaptations in order to grow successfully in new territories. When crop species moved beyond their original ecological boundaries they endured novel environmental and seasonal conditions, and annual temperature patterns (Lister et al. 2009). Post-domestication genetic and often morphotypical changes were crucial for crop survival in varied latitudes and altitudes (Fuller & Lucas 2017; Liu et al. 2017). In other words, changes in climatic conditions as crops dispersed from their areas of domestication drove alterations in a variety of their genes so that they could grow and survive in new environments. These genetic adaptations to new environments included resistance to certain diseases, as well as adaptation to ultraviolet (UV) intensity, changes in vernalization requirements and flowering times (Dawson et al. 2015). For example, in south-west Asia, where all European Neolithic crops are presumed to have been
domesticated, the growing season for crops is terminated by summer aridity, as the plants need to complete growth while the ground is still moist (Lister et al. 2009). However, in the north, away from their original domestication regions, crops normally receive rainfall in the early summer rather than winter, thus becoming increasingly maladaptive as the growing season shifts forward into summer (ibid.). Lister et al. (2009, 2) suggests: “that the rate of agricultural spread northwards might have been determined not just by human social and economic factors, but also by the continued evolution and adaptation of the crop plant itself in relation to altered seasonalities.”

This paper reviews the origins of agriculture in the eastern Baltic region from a plant adaptation point of view. It is suggested that for genetic adaptation of a crop plant to new environments, changes in day length and vernalization times could have been some of the reasons that dramatically slowed down the introduction of successful crop cultivation in this region.

**Current agricultural evidence in the East Baltic**

The existing cereal pollen data from Lithuania reports the presence of Cerealia-type pollen dated back to as early as 5500/5300 BC (Stančikaite et al. 2002) and even 5600 BC for Estonia (Poska & Saarse 2006). In addition to pollen data, some authors report the presence of domestic animals (Daugnora & Girininkas 2004), macro-remains of cultivated plants and agricultural tools at Neolithic sites in Lithuania (Rimantienė 1992a; 1992b; 1992c; 1996) and Latvia (Lõugas 2006). A recent review by Griškėdis and Motuzaite Matuzeviciute (2017), however, has challenged those claims, concluding that there is no substantial evidence to suggest that human populations in the East Baltic practiced agriculture during the Neolithic, ca 5500/5300 – 1800 BC. Cerealia-type pollens which appear in Lithuania during this period and are represented in very low numbers and could well be contaminates from upper, younger layers displaced during the sample coring process, or carried in by wind from other agricultural societies hundreds of kilometres away (Griškėdis & Motuzaite Matuzeviciute 2017). Moreover, wild plants that produce pollen similar to domestic grasses grow in the northern hemisphere, thus making it hard to separate between the species (Behre 2007). The pollen grain count, undoubtedly that of Cerealia-type, increases only during the Bronze Age period, showing the growing importance of Poaceae-family plants (Griškėdis & Motuzaite Matuzeviciute 2017). Similarly, tools clearly related to agriculture are present in the eastern Baltic region only during the Bronze Age period, constituting of flint sickle blades, stone hoes, mortars and pestels (ibid.).

In the whole eastern Baltic region, we currently do not have any macrobotanical remains of domesticated cereal dated to the Neolithic period. A variety of cultivated plants had been previously identified at 4th–3rd millennia BC Šventoji sites in western Lithuania (Rimantienė 1992a; 1992b; 1992c). Those domesticates, however, have recently been re-dated or re-identified by archaeobotanical specialists,
changing our previous notion about local cultivation. It appears that the seeds of cultivated *Setaria italica* identified in Šventoji, instead belong to the wild *Setaria viridis* species, which is indigenous to all of Eurasia (Tutin et al. 1996), while all the seeds attributed to *Cannabis* genus belonged to the yellow water-lily (*Nuphar lutea*) (Grikpėdis & Motuzaite Matuzeviciute 2017). The only carbonized grain from the Šventoji site originally identified as Emmer wheat was, after archaeobotanical revaluation, re-identified as rye and its direct radiocarbon date has shown it to belong to the 20th century AD rather than BC (Piličiauskas 2016).

Similar situations with dating or identifying plant remains exist in the whole eastern Baltic region where plant remains were collected and identified as domestic, but now their remains have been lost in museum archives and their identification can no longer be tested. Some domestic cereal impressions, such as barley found in Late Neolithic pottery in Estonia (Lang 2007; Kriiska 2009) are also hard to check chronologically. Moreover, pottery impressions do not necessarily imply local plant cultivation as pottery vessels could have been made elsewhere and imported from neighbouring agricultural societies (Motuzaite Matuzeviciute 2012). The only radiocarbon dates that have been obtained so far directly on cereal grains are from two sources: the Niuskalasite in Finland where a barley grain was dated to 1600–1250 BC (Vuorela & Lempiäinen 1988), and Lithuania where two barley grains were dated to ca 1400–1200 BC (Piličiauskas 2016; Grikpėdis & Motuzaite Matuzeviciute 2017).

The evidence for Neolithic domestic animals in the eastern Baltic region is also ambiguous. Currently, the chemical analysis of pottery vessels from the Late Neolithic period (2700–2400 cal BC) in western Lithuania (Nida site) have shown that only two of them could potentially have contained ruminant dairy (Heron et al. 2015). Some solitary finds of sheep/goat bones, such as a chisel made from the bone of a domesticated goat or sheep, was found in the Zvejnieki burial 137 (Lõugas 2006) and has not yet been radiocarbon dated (Meadows et al. 2016). Instead, the only direct dates that were done on ovicaprid and cattle bones from Neolithic period sites in Lithuania have generated much later dates, attributing them to the Middle Bronze Age (Piličiauskas et al. 2016). In Finland, out of 19 dated bones of domestic animals belonging to the Kiukainen Culture, 13 were attributed to a much later period AD and only one burnt bone, identified as sheep/goat was dated to ca 2000 BC, while the rest of the bones were attributed to possibly domestic animals belonging to the 15th century BC (Bläuer & Kantanen 2013). The existence of such a small amount of pots with dairy fat (that could well be imported) and the absence of the Neolithic domestic animals questions the importance of animal products in the Late Neolithic societies of the East Baltic. Therefore, despite the human inflow of the Corded Ware Culture from potentially agro-pastoral societies in the north Black Sea region (Haak et al. 2015; Jones et al. 2017; Mittnik et al. 2018), agriculture did not start to develop in the eastern Baltic for another thousand years.
Why barley: Genes at fault?

It is probably not a coincidence that the currently known earliest cultivated plant from the East Baltic belongs to a barley species. The remains of cereals consisting almost exclusively of barley have been reported from 2nd millennium sites in Lithuania (Kvietiniai), Latvia (Kreiči), Estonia (Iru) and Finland (Niuskala, Kitulansuo, Jātinhaudanmaa, Laihia Alatalo, Eura Luistari) (see Table 1). Only during the 1st millennium BC wheat, false flax, millet and legumes join the spectrum of cultivated crops.

Barley can be cultivated in a wide range of environments and it is one of the most adaptable cereals. It can be cultivated in the Arctic Circle at up to a latitude of 70° (Vorren 2005) or in the highlands of Tibet at 5000 masl (Knüpffer et al. 2003). Barley yields are generally considered to vary less under changing weather conditions than those of wheat and most other small grains (Dawson et al. 2015). However, barley adaptability is not only due to its higher tolerance to poorer soils, but mainly due to various genetic mutations that allow barley to grow in different environments. Barley is a diploid rather than polyploid, like wheats or millets, and therefore it is easier to manipulate the selection process. Various mutations have arisen in barley since domestication, facilitating its planting in spring at more northerly latitudes (Jones et al. 2011). Still today, in the northern latitudes and in the highlands, for example, barley is mainly a summer crop (Knüpffer et al. 2003). Once barley moved into northern latitudes with cooler climates and different day length patterns, the genes responsible for photoperiod time and vernalization time had to be silenced to permit its growth (Jones et al. 2012). The mutation of the silenced barley genes probably occurred in the Near East where it was domesticated (Jones et al. 2008). However, these same mutants had to be selected upon once barley reached the north, because only then could barley be successfully cultivated with minimal risk to the harvest. Responsiveness to long days, regulated by the ppd-H1 gene, is an advantage to plants in dryer regions as seasonal patterns (day length and frost) are the main hormonal triggers, thus allowing early flowering, pollination and grain filling to occur before a dry summer (Lister et al. 2009). Therefore, most wild barleys in south-west Asia are day-length responsive as they have to mature their seeds before the summer drought. On the other hand, non-responsiveness to long days (when ppd-H1 is silenced) allows plants to flower later in the growing season. For example, wild barley (*H. spontaneum*) in Israel flowers in early March while the spring barleys flower from early June to middle July in northern Sweden (Lister et al. 2009). In northern latitudes the growing season shifts forward into the summer, and therefore barley in the north was under pressure to become spring-sown rather than autumn-sown in order to adjust better to the change of seasonality and temperature patterns and become photoperiod non-responsive, by muting the Ppd-H1 gene (Lister et al. 2009). As mentioned above, spring-sown barleys also have silenced vernalization
Table 1. The records of the earliest crop species from the East Baltic dated between the 2nd – 1st millennia BC. The distribution of species show that *Hordeum* sp. is almost exclusively the only cereal species found during the 2nd millennium BC, while during the 1st millennium BC other crop species join the agricultural package (this table has been modified after Griķpēdis and Motuzaite Matuzevičiute, 2017 publication)

<table>
<thead>
<tr>
<th>Country</th>
<th>Site</th>
<th>Species</th>
<th>Chronology</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lithuania</td>
<td>Kvietinia</td>
<td><em>Hordeum vulgare, Cerealia</em></td>
<td>1392–1123 cal BC</td>
<td>Griķpēdis &amp; Motuzaite Matuzevičiute 2017</td>
</tr>
<tr>
<td></td>
<td>Turlojiške</td>
<td><em>Panicum miliaceum</em></td>
<td>908–485 cal BC</td>
<td>Antanaitis &amp; Ogrinc 2000</td>
</tr>
<tr>
<td></td>
<td>Nida</td>
<td><em>Hordeum</em></td>
<td>Ca middle of 4th–3rd millennium BC</td>
<td>Heydeck 1909; Chronology: Rimantienė 1992a; Piličauskas 2016</td>
</tr>
<tr>
<td></td>
<td>Šiutkalns</td>
<td><em>Hordeum vulgare, Triticum dicoccum, Panicum miliaceum, Pismum sativum, Camelina sativa, Vicia faba</em></td>
<td>650 BC – AD 50</td>
<td>Rasins &amp; Taurina 1983; Chronology: Oinonen et al. 2013</td>
</tr>
<tr>
<td></td>
<td>Mūkukaļnu</td>
<td><em>Hordeum vulgare, Triticum aestivum, Vicia faba</em></td>
<td>1st millennium BC</td>
<td>Rasins &amp; Taurina 1983</td>
</tr>
<tr>
<td>Estonia</td>
<td>Iru</td>
<td><em>Hordeum vulgare</em></td>
<td>2700 BC</td>
<td>Poska &amp; Saarse 2006</td>
</tr>
<tr>
<td></td>
<td>Asva</td>
<td><em>Hordeum, Triticum, Avena</em></td>
<td>900–500 BC</td>
<td>Lang 2007</td>
</tr>
<tr>
<td>Finland</td>
<td>Niinskala</td>
<td><em>Hordeum</em></td>
<td>1891–1018 cal BC</td>
<td>Vuorela &amp; Lempiäinen 1988</td>
</tr>
<tr>
<td></td>
<td>Kitulansuo</td>
<td><em>Hordeum vulgare</em></td>
<td>1400–1048 cal BC</td>
<td>Lavento 1998</td>
</tr>
<tr>
<td></td>
<td>Laihia Alatalo</td>
<td><em>Hordeum vulgare var. vulgare, Hordeum vulgare, Avena sp.</em></td>
<td>830–550 cal BC, 2 other grains fall to ca 1000–500 cal BC</td>
<td>Holmblad 2010</td>
</tr>
<tr>
<td></td>
<td>Eura Luustari</td>
<td><em>Hordeum vulgare</em></td>
<td>2560 ± 55 BP, i.e. 780–562 cal BC</td>
<td>Lehtosalo-Hilander 1999</td>
</tr>
</tbody>
</table>
The possible geographic margin effect on the delay of agriculture introduction

The delays of the spread of agriculture to Scandinavia have been explained as the time taken for the crops to adapt to novel climatic conditions, such as altered temperature regimes and day-lengths (Lister et al. 2009). The situation with wheats is similar, although unravelling the genetics has been more complex because of the multiple genomes found in most wheats (Fuller & Lucas 2017). However, similarly to barley, adaptive processes were involved in these cereals as agriculture moved north through Europe (Cockram et al. 2007).

Discussion

Spring-sown crops become visible in various regions of Europe only around the Bronze Age ca 3000 BC and the absence of spring-sown varieties before then is likely to have been one of the factors that contributed to agricultural failures along the northern margins of agriculture (Fuller & Lucas 2017, 321). Early crop movements to northern latitudes probably encountered higher levels of harvest failure before reaching a balance where growing crops was worthwhile for the local inhabitants. Therefore, it has been argued that the rate of agricultural spread northwards might have been determined by the continued evolution and adaptation of the crop plant itself in relation to altered seasonalities (Lister et al. 2009). Early crops in the northern latitudes had to mutate becoming spring-sown rather than winter-sown as such cereals with silenced genes had more chances to produce a surplus in harvest. Winter cereals could technically also grow in northern latitudes: we know they eventually do. However, the spring varieties are more common and better adapted to new environments. In prehistory, with poor agricultural techniques, autumn-sown variety cultivation was much riskier as prolonged winters and fluctuating temperatures after crops sprouted could potentially fully destroy the harvest. Halstead (1989) proposes that in areas where crop yields were reduced (or where crops failed altogether) because crops were not adapted to local climates, humans would adopt a broad-base subsistence strategy which relied less on crops and more on animal husbandry, or hunting, fishing and foraging wild resources. We see a similar situation at the Kvietiniai site where the earliest barley grains in Lithuania were identified. From multiple investigated contexts we see just a few barley grains, allowing us to speculate that agriculture was not established and that human populations were relying mainly on wild resources instead (Grikpėdis & Motuzaitė Matuzevičiute 2017). This view does not contradict the Zvelebil and Rowley-Conway (1984) three-phase model. It was partly a human choice not to persist in growing cereal during the Neolithic (availability stage) as plants did not do well. Though the
substitution stage some grain selection for spring-sown varieties allowed agricultural expansion, until the consolidation phase where crops constituted a large percentage of the human diet, becoming well adapted to local climates and mainly spring-sown.

As seen from the archaeobotanical review on agriculture in the eastern Baltic region presented above, the pattern of reliance on hunting-gathering and maybe small-scale farming prevailed there until the Bronze Age. During the Final Bronze Age and the Early Iron Age we start seeing a much higher diversity of crops, indicating a better adaptation to the environment and reduction of risk of crop failure. During this period, we can state that agriculture in the East Baltic became established, reaching the consolidation phase. This period strongly correlates with social changes, population growth and the formation of fortified settlement sites (Lang 2007; Motuzaite Matuzeviciute 2015). A high abundance and wide variety of crop species have been found in multiple archaeological sites from this period. The crops include *Hordeum vulgare*, *Triticum dicoccum*, *Triticum spelta*, *Camelina sativa*, *Panicum miliaceum*, *Pisum sativum* and cultivated Fabacea (Grikpėdis & Motuzaite Matuzeviciute 2017).

Judging from weed species and some key crops, as for example a short growing broomcorn millet crop, we know that populations during the Final Bronze Age period were mainly cultivating spring-sown crops. A good example illustrating this could be drawn from the Lake Luokesa 1 site in eastern Lithuania. There, archaeobotanical investigations were carried out on uniquely preserved waterlogged environment, and plant remains were dated to ca 600 BC (Motuzaite Matuzeviciute 2007; Pollmann 2014). From the 23 taxa identified, 91% of the weed taxa belong to summer cereals/root crops or ruderal plants (Pollmann 2014). Both *Camelina sativa* (in phyllosphere) and legumes (in roots) found at the Lake Luokesa site contain nitrogen-fixing bacteria that enriches the soil, thereby facilitating plant adaptation and growth (Hayman 1986; Lovett & Sagar 1978). Such nitrogen-fixing plants facilitate the growth of other summer crop species, contributing to a better adaptation to the environment and the production of a surplus harvest. This process inevitably had a pronounced effect on economical changes during the Late Bronze Age – Early Iron Age period in the East Baltic.

As it has been already suggested by previous research, the introduction of day-length non-responsive type crops helped to facilitate the relatively late establishment of successful agriculture (Jones et al. 2012). Similar patterns of crop dispersal are also seen along the east-west axis of Eurasia, where agriculture dispersal was postponed by thousands of years in mountainous areas before reaching China. The earliest evidence of south-west Asian crops in the mountain ranges separating China from Central Asia dates back only to the Bronze Age (the middle of the 3rd millennium cal BC) for wheat (Doumani et al. 2015) and the early 2nd millennium cal BC for barley (Motuzaite Matuzeviciute et al. 2015). Subsequently with some delay (at the beginning of 2nd millennium cal BC) wheat
and barley were dispersed across the western regions of China (Stevens et al. 2016; Liu et al. 2017). It has also been argued that one of the key factors for the delay in arrival of south-west Asian crops into China was the interposition of marginal environments such as the Tibetan plateau (D’alpoim Guedes et al. 2014) and the Central Asian mountain ranges (Spengler et al. 2014); in order to cross them crops had to undergo major genetic transformations, mainly to become spring-sown (Liu et al. 2017).

**Conclusive remarks**

This paper discusses the possible reasons why the introduction of agriculture in the East Baltic was delayed until the Bronze Age (current state of knowledge which can be modified with further archaeobotanical research), while in southern Scandinavia, for example, agriculture has long been an established phenomenon. In addition to reasons postulated by previous researchers, this paper proposes that genetic transformations and adaptations of cereals to new environments, including climatic and day length changes, also contributed to the delay in agriculture spreading to this region.

Barley might have been one of the first cereals to acquire the silenced haplotypes of important flowering-time and vernalization genes, becoming spring-sown. This haplotype gave an advantage to be selected in northern latitudes for cultivation. Later, during the Late Bronze Age, the number of crop species had increased as more spring-sown cereals joined the cultivar group. Adaptation to climatic changes was facilitated by nitrogen-fixing cereals, allowing the generation of surplus harvests and contributing to social change in the region.

In the end it is important to emphasize that the dispersal and acquisition rate of agriculture in the eastern Baltic region is a very complex phenomenon that is driven by climatic fluctuations, human choice, and also the rate of plant genetic transformation and adaptation to new environments. By looking at this phenomenon holistically we will be able to gain a more complete picture of agricultural dispersal and the reasons for its late arrival in the Baltic region.

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Giedre Motuzaite Matuzeviciute

GEOGRAAFILINE ÄÄREALA VILJELUSMAJANDUSE HILISE JUURDUMISE VÕIMALIKU PÕHJUSENA BALTIKUMIS

Resümee

graafilistel laiustel ning pikkustel väga olulisteks (Fuller & Lucas 2017; Liu et al. 2017). Teisisõnu, erinevused klimaatilistes tingimustes väljaspool kodustamise piirkonda kutsusid esile mitmesuguseid geenimuutusi, mis tagasid taimede kasvu uutes keskkondades. Seesugused geneetilised muutused tõid muuhulgas kaasa ka taimede resistenttsuse teatud haiguste ja põua vastu ning kohanemise senisest erinevate idanemistingimustega, UV-intensiivsuse ja õitseajaga (Dawson et al. 2015).

Käesolevas artiklis on käsitletud viljelusmajanduse algust Baltikumis taimede kohanemise seisukohalt. On leitud, et taimede geneetiline kohanemine kontinentaalse kliima, teistsuguse päevapikkuse ja idanemistingimustega võis olla üks põhjusi, mis dramaatiliselt aeglustas teraviljakasvatuse arengut selles regioonis.