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## The trans-Eurasian crop exchange in prehistory: Discerning pathways from barley phylogeography

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### ABSTRACT

A number of crops that are of global importance today, including wheat (*Triticum* spp) and barley (*Hordeum vulgare*), were domesticated in Southwest Asia between 10,000 and 11,000 years ago and subsequently spread through the Old World, into Europe, North Africa and eastwards across Eurasia. Their routes of expansion have been a focus of debate and are increasingly being revealed by widespread dating of archaeobotanical remains from across Eurasia. Of particular interest is work by Zhao (2009) who proposed three routes for the spread of wheat into China: firstly, across the Eurasian Steppe, second by sea from India to the east coast of Eurasia and third, along the Hexi Corridor, which forms part of the Silk Road in western China. Molecular genetic analysis of cereal landraces have also elucidated routes of expansion of cereal cultivation and, in addition, have revealed how crops adapted to changing environments as they moved away from their centres of domestication. Genes involved in flowering time genes have been a particular focus of these studies, including the photoperiod response gene *Ppd-H1* in barley, which controls flowering in response to increasing day-lengths in the spring. In this paper we present a phylogeographic analysis of Old World landrace and wild barley, through the analysis of a portion of the *Ppd-H1* DNA sequence. We discuss the geographic distribution of different haplotypes of this gene across Eurasia in the light of Zhao (2009)'s three routes and what it potentially reveals about trans-Eurasian pathways of contact between early farming communities.

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### 1. Introduction

A number of crops domesticated in southwest Asia between 10,000 and 11,000 years ago have now become global crops of significant economic importance; these include wheat (*Triticum* spp.) and barley (*Hordeum vulgare*). During prehistory, these two crops spread through the Old World, into Europe, North Africa and eastwards across Eurasia, while at a similar time other cereal domesticates originating in China (*Panicum miliaceum* and *Setaria italica*) spread towards the west (Jones et al., 2011a). The routes of expansion of these southwest Asian crops, and by implication the

networks of contact between prehistoric farming communities, has been a focus of debate (e.g. Zhao, 2009; Fuller, 2011a, b; Jones et al., 2011a; Spengler et al., 2014). This debate is mirrored by discussion of the spread of east Asian crops toward the west (Motuzaitė-Matuzevičiute et al., 2013, 2015). Widespread recovery of archaeobotanical remains using flotation at many archaeological sites across Eurasia and accurate radiocarbon dating of single grains has revealed an increasingly detailed picture of how and when crops reached particular regions and the routes by which they spread. Determining how crops adapted to novel environments as they were moved from centres of domestication is also informative. In the past decade a number of phylogeographic studies of extant crop landraces have also sought to address these questions, many with a particular focus on genes involved in flowering time determination, for example vernalization and photoperiod response genes in wheat and barley (e.g. Jones et al., 2008; Cockram et al., 2011; Saisho et al., 2011; Kippes et al., 2015).

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Archaeological evidence from the Near East shows that wild barley was being utilized for at least 10,000 years before morphological domestication (Hillman et al., 2001; Weiss et al., 2004). Non-brittle two-rowed (i.e. domesticated) barley has been identified at Near Eastern sites such as Tell Abu Hureyra in the early 9th millennium BC (Hillman, 1975); and Tell Aswad in the 8th millennium BC (van Zeist and Bakker-Heeres, 1985). Non-brittle six-rowed barley has been identified at Ali Kosh, Iran, in the 8th millennium BC. Records of naked barley, mostly from six-rowed forms, appear at Ali Kosh from the 7th millennium BC (Helbaek, 1969). By the beginning of the third millennium BC, wheat and barley had spread across the Old World, and were being cultivated in Europe, North Africa and eastwards into South Asia and China (Helbaek, 1969; Zohary and Hopf, 2000; Jones et al., 2011a, 2012, 2013). Much of the literature has focused on the spread of wheat species, since this grain is predominates in the archaeobotanical records of the period. However, barley is frequently found alongside wheat in archaeobotanical assemblages in the Old World; two Southwest Asian staples travelled together as part of the 'Neolithic package' which also included sheep (Barker, 1985).

Evidence for the arrival of the southwest Asian cereals in North Africa is quite sparse, with flotation and dating of archaeobotanical remains occurring only recently. Morales et al. (2013) suggest that the similarity in radiocarbon dates in domesticated plant species from Neolithic sites in North Africa and the Iberian Peninsula is evidence for synchronous spread of agriculture along both shores of the western Mediterranean, where barley dates from the 7th millennium BP.

Barley cultivation reached China by 4500 BP (Flad et al., 2010), and was found at altitudes of at least 3600 m in the Tibetan Plateau by 3500 BP (Chen et al., 2015). During the 3rd millennium BC barley is recorded in Korea (Crawford and Lee, 2003) and middle Jomon Japan (Matsui and Kanehara, 2006). The archaeobotanical record suggests that cultivation of wheat and barley, and the east Asian crop, millet, spread to the Eurasian steppe later in prehistory (Ruehl et al., 2015; Spengeler, 2015). With flotation and advances in AMS radiocarbon dating technologies, it has been possible to directly date archaeological cereal remains. Such data led Zhao (2009) to propose three different routes for the spread of wheat (and by inference barley) into China around 4000 BP:

- (1) The Eurasian Steppe Route, in which wheat (and other southwest Asian package items including barley and sheep) spread to China by means of the vast steppe traversing Central Asia, southern Siberia and the Mongolian highlands. Archaeological evidence lends support to Zhao (2009) northern steppe route accounting for contact between east and west Eurasia, and a pathway of movement of resources and ideas about horse-riding, sheep herding, metal technology (Chernykh, 2008) and the farming of such cold hardy crops as barley. The latitude of such a steppe route would be expected to involve cereals non-responsive to increasing daylengths in the summer, as will be discussed below, and lead to shared genetic patterns from west to east.
- (2) The Sea Route, where wheat spread into China by boat from South and Southeast Asia. Wheat was a major crop of the Indus Civilization by this time (Constantini, 1984). At the time Zhao's paper was written, the earliest dated wheat was found in Shandong and Fujian Provinces, on the east coast of China; more dates have now indicated that the earliest dates for wheat are inland in Gansu Province (Dodson et al., 2013). Betts et al. (2014) consider this coastal route unlikely as it would take the western cereals through landscapes and climates not suitable for their cultivation.

- (3) The Silk Road, where wheat was introduced into China along the Hexi Corridor, which during historical periods became an important route between Central Asia and North China. This is topographically the most convenient route East-West and it is highly likely that this route was used during prehistory as well, with many of the earliest dated wheat remains come from this region (Betts et al., 2014).

In practice, there may have been a combination of different routes. The initial hypotheses of Zhao (2009) allow us to support or challenge some of the potential routes in the spread of the South-west Asian crops through Eurasia.

Archaeological and archaeobotanical data pertaining to the domestication of crops and the spread of agriculture is being supplemented with molecular genetic data derived from living cereal landraces and wild progenitors (e.g. Saisho and Purugganan, 2007; Poets et al., 2015), from herbarium specimens (e.g. Lister et al., 2009) and, more rarely, from archaeological material (Li et al., 2011; Smith et al., 2015). These studies are revealing the locations and number of domestication events, the identity and function of 'domestication genes', such as those determining the brittle/tough rachis trait, as well as how and by what routes cereals spread from their centres of domestication. Various reports have argued that barley was domesticated more than once and in different areas, and that domesticates from each area spread via different trajectories (e.g. Morrell and Clegg, 2007; Saisho and Purugganan, 2007). Different types of genetic markers have been used in phylogeographic studies; e.g. analysis of neutral markers such as microsatellites, or simple sequence repeats (SSRs), have revealed population structure relating to the spread of agriculture across Europe and North Africa (e.g. Jones et al., 2011b; Jones et al., 2012; Oliveira et al., 2012; Jones et al., 2013) and the analysis of single nucleotide polymorphisms (SNPs) in expressed genes has aided in our understanding of how, for example, crops adapt to novel environments by modifications to flowering-time pathways (Jones et al., 2008).

### 1.1. The role of environmental adaptation in the spread of agriculture

During prehistory barley cultivation spread into climatically novel environments, ranging from cold temperate regions of northern Eurasia to sub tropical regions of South Asia, and high altitude regions of the Tibetan Plateau. In order that plants may complete their life cycle it is essential that flowering coincides with favourable seasonal conditions, enabling plants to avoid damage through extremes of temperature or drought (Cockram et al., 2007). Work by various authors has shown that variants in different genes involved in flowering time have been important in the adaptation of barley to novel environments. These genes in wheat and barley include those involved in photoperiod response, (e.g. *Ppd-H1*) in which flowering is triggered in response to long days (e.g. Turner et al., 2005; Jones et al., 2008), and vernalization, where flowering is initiated after a period of chilling in the vegetative state, e.g. *Vrn1* (Yan et al., 2003), and *Vrn2* (Yan et al., 2004). Understanding the ecological drivers of cereal cultivation and successful completion of lifecycle (i.e. flowering and seed set) is an important factor in understanding patterns of agricultural spread.

The *Ppd-H1* gene has been the subject of previous research by Jones et al. (2008) on European landrace barley and Near Eastern wild barleys, and Stracke et al. (2009) on a set of world-wide barleys. Analysis of the *Ppd-H1* gene by Jones et al. (2008) identified the causal single nucleotide polymorphism (SNP) that turns off the trigger to flower in response to long days, and the distribution of the wild type and mutant form shows a geographic cline, with a

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