



The Domestication of the Seasons: The Exploitation of Variations in Crop Seasonality Responses by Later Prehistoric Farmers

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Discussions of domestication and its associated genetic traits has focused upon dispersal mechanisms, for example in the rachis structure of cereals. Here we consider another trait of importance to domesticated crops – their seasonality response. We particularly consider flowering response to changing daylength, and how that relates to domesticated species that are carried by farmers considerable distances from their regions of origin. We consider the implications of cultivating crops in regions whose seasonality patterns contrast with those of the crop's region of origin, and consider the consequent genetic changes. Reference is made to the particular case of barley, and a discussion of archaeogenetic research into its photoperiod response mechanism is provided.

Keywords: photoperiod response, flowering time, archaeobotany, archaeogenetics, Bronze Age, irrigation, multicropping

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INTRODUCTION

In many grain crops, the principal feature used to distinguish wild from domesticated forms is the loss of the plant's pre-existing dispersal system. That ancestral system depends upon regions of stem tissue becoming brittle once grain filling has reached completion. The evolutionary loss of that attribute effects a transition between "brittle-rachis" forms, whose grains can disperse by natural means, and "tough-rachis" forms, in which dispersal depends upon human agency. As with other domestication features, the transition from a tough to brittle rachis is thought to be a protracted process; it took time for domestication phenotypes to arise and become fixed in populations. It was also largely driven by unconscious human selection (e.g., Purugganan, 2019). Within studies of the human past and crop domestication, considerable emphasis has been placed upon the brittle to tough rachis transition, and has been taken by some to mark the transition between hunter-gatherers and farmers (cf., Hammer, 1984).

Such a transition is not as singular as it may at first seem. There are other episodes in crop plant evolution in which certain genetic mutations have led to different phenotypes and a novel dependency upon human agency, as well as new opportunities for exploitation and control. Two of these episodes relate to seasonality response mechanisms by which seed plants optimize their reproduction by flowering and fruiting during the most suitable season of the annual cycle. Alterations in responses to environmental variables also have significant consequences for people-plant relationships, the topic explored in this article.

SEASONALITY RESPONSES IN PLANTS

Plant growth is sensitive to a wide variety of environmental attributes that in turn are subject to predictable seasonal fluctuation. The pattern of that sensitivity varies considerably between and within plant taxa. In cereals, changes in certain environmental variables have been shown to trigger different life stages. The best studied of these are the initiation of flowering in response to: (i) lengthening days in the spring (photoperiod sensitivity), and (ii) a period of cold temperatures in the autumn (vernalization requirement). These two triggers for plants to flower are the most discussed in literature about the effects of the environment on the spread of crops away from their regions of domestication (e.g., Turner et al., 2005; Cockram et al., 2007; Liu et al., 2017). While the phytochemistry and genetic control of the triggering mechanisms may be widely shared across taxa, in the case of photoperiod sensitivity, the critical daylengths to which they respond vary greatly among species and within the same species, allowing for a wide array of seasonality responses across different ecosystems of the world (Jackson, 2009).

Flowering at the optimal time is critical for a plant to complete its lifecycle, and in the case of agronomically important plants such as cereal crops, maximizing yield and quality. The optimal time for flowering in cereals is determined by a balance between the water required at different life stages, such as vegetative development and grain filling, and the avoidance of deleteriously low temperatures. If a plant flowers too early, especially in temperate and northerly latitudes, flowers may be damaged by frost. If it flowers too late, particularly in more southerly latitudes and continental interiors, high temperatures and a water deficit could result in restricted grain formation. Higher plants have an endogenous “circadian clock” that guides the plant as to what season it is and when is the optimal time for various transitional phases, such as flowering. This is coordinated through several interlocking gene families (Harmer, 2009). Through a variety of photoreceptors, the circadian clock senses changes in environmental variables such as temperature and light. Photoperiod-dependent flowering is regulated *via* the circadian clock sensing changes in daylength, Imaizumi (2010); in wheat and barley this is controlled by the circadian clock *Ppd* gene family (Turner et al., 2005).

As indicated above, the two most frequently discussed triggers driving flowering time are daylength and temperature. They are not the only triggers, and indeed the sensitivity of the plant to numerous factors is determined by both adaptive evolution at the genotypic level and phenotypic plasticity. The latter is defined as the ability of a given genotype to produce distinctive phenotypes under varied environments (e.g., Weiss et al., 2009). Research has shown that there is enormous plasticity in flowering-time behavior among cereal crops, which ensures flowering is only induced under optimal conditions (Hill and Li, 2016). These adaptive responses differ both within and between species, culminating in a complex picture, particularly in relation to local agronomic terminologies of, for example, “spring crops” and “winter crops.” However, they are significant

triggers, and ones whose genetic basis has been well studied. Two of the major gene families that control the transition from a vegetative to a reproductive phase are the circadian clock *Ppd* genes, relating to photoperiod response (Cockram et al., 2007; Jones et al., 2008), and *Vrn* genes relating to vernalization (e.g., Distelfeld et al., 2009). The focus within the remainder of this paper is upon the first of these, relating to photoperiod response, and the distinction between short day and long day plants.

Short day plants (that flower in response to a shortening of the photoperiod) across the globe include the domesticated plants: maize, *Zea mays*, and common bean, *Phaseolus vulgaris* (Central America; Bhakta et al., 2017; Brambilla et al., 2017); sorghum, *Sorghum bicolor*, and cowpea, *Vigna unguiculata* (Sub-Saharan Africa; Lush and Evans, 1980; Brambilla et al., 2017); rice, *Oryza sativa* and soybean, *Glycine max* (Southern China; Nakamichi, 2015; Choi and Purugganan, 2018); and broomcorn millet, *Panicum miliaceum*, and foxtail millet, *Setaria italica*, (North China; Doust et al., 2017). These plants are adapted to accumulate biomass over the summer season and flower later in the growing season.

In contrast to the many regions of domestication in which “short day” crop plants predominate, there is one geographical center of domestication in which a number of long day crop plants play a significant role, and that is the “Fertile Crescent” of Southwest Asia. In this region, the various species and varieties of wheat, *Triticum* spp., barley, *Hordeum vulgare*, rye, *Secale cereale*, oat, *Avena sativa*, and pea, *Pisum sativum*, are long day plants (Nakamichi, 2015), which flower in response to a lengthening of the photoperiod. These plants are adapted to accumulate biomass when both temperatures and insolation may be sub-optimal but at least when there is sufficient available water, which is not the case in the ensuing hot summer season. This generally means that they flower early in the growing season.

The evolutionary history of variants in these flowering-time genes is probably deep in comparison with the relatively short timescale of the emergence of agriculture in different regions of the world. For example, certain wild barley populations have been shown to possess the non-responsive allele of the photoperiod response *Ppd-H1* gene, and are the ancestors of the non-responsive domesticated barley found in Europe today (Jones et al., 2008). This mutation would not have necessarily conferred an adaptive advantage in the Near East and thus may not have been selected for in early episodes of Neolithic agriculture, prior to its spread out of the region of domestication, since the seasonality of the environment prior to the spread of agriculture was broadly similar to that of the wild plant ancestors. During the Neolithic Period, however, and particularly during the subsequent Bronze Age, Old World domesticates spread significant distances from their place of ancestral origin, in some cases to regions in which the seasonality constraints would have been very different. In more temperate climes, non-responsive variants of the *Ppd-H1* were better adapted to the longer and cooler summers. By the middle of the second millennium BC, such crop movement had become substantial, with the consequence that many crops were being cultivated far from

their region of origin, where they continue to be cultivated today (Jones et al., 2016).

SWITCHING OFF SEASONALITY TRIGGERS AND CONTROLLING WATER AVAILABILITY

An overview of the contemporary genotypes of Old World grain crops reveals something resonant with the brittle rachis character. The tough rachis character had been selected for in the context of farming, lending farmers some control over dispersal and harvesting. Likewise, in many varieties of different grain crops, mutations in seasonality response genes that have led to the switching off of the flowering response to environmental cues have been selected within a farming context, lending farmers some control over crop scheduling. Examples of these seasonality genes being switched off have been recorded in a range of domesticated plant taxa, including maize, soybean, tomato, and wheat (Lin et al., 2021). Such crops can instead flower at various times of the year, provided sufficient biomass has accumulated, opening up new options for their exploitation within agriculture. The occurrence of mutations switching off such genes has consequently contributed toward agriculture spreading out from its regions of origin, into environments with completely different patterns of seasonality.

How advantageous these mutations might be for the farmer depends upon how much the farmer can control growing conditions. In the case of short day crops, the factor limiting growth and driving evolution of the short day response is insolation, over which farmers have very limited control. The facility to grow such crops in a “displaced” season may in principle be useful as part of a multi-cropping cycle, but those crops will be growing in suboptimal conditions. In the case of long day crops, however, one of the major factors limiting growth and driving evolution of the long day response is water, over which farmers, certainly by the Bronze Age, were able to exert considerable control, and thus maintain optimal conditions for plant growth.

The place of large scale water management in cultural evolution has a long history of study, notably in relation to the theories of Wittfogel (1957) concerning hydraulic and hydro-agricultural societies, theories which have on several occasions been revisited and reassessed (cf., Price, 1994). What remains uncontested is the archaeological evidence for significant investment in irrigation systems in various regions of the Old World from the second millennium BC onward. Those regions include Egypt, Mesopotamia, the Indus Valley and China, for each of which there now exists a significant corpus of archaeobotanical evidence for crops. One common feature clearly emerges from that crop evidence. As the second millennium BC progressed, a significant component of the crop repertoire in each of these regions comprises long day plants originating from Southwest Asia, most notably, wheat and barley.

Even before the elaborate irrigation systems that grew up during the second millennium BC around major Old World river valleys, water could have been significantly controlled by the

construction of relatively small-scale ditches and dams. Water-management had been well within the reach of human control since at least the beginnings of farming. It follows that long day crops have a particular utility in water-managed systems, to which they are pre-adapted. While it is certainly the case that any crop with seasonality responses switched off can in principle be deployed to artificially extend growing seasons, it is particularly the case that long day plants are well suited to such environments, as one of the major factors limiting to growth is water, which as indicated above, the farmer may be able to control. Hence, each of the Bronze Age civilizations of the Old World that managed water to extend season length did so with long day grain crops originating in Southwest Asia.

BRONZE AGE CROP MIXTURES ACROSS THE OLD WORLD

Water management has an especially long history within Egypt (Butzer, 1976), where the early crops, in particular emmer wheat (*T. dicoccum*) and barley, originated from neighboring Southwest Asia. This cultivation within Egypt of emmer and barley is contemporaneous with another long episode of plant exploitation further south within the Nile Valley in modern day Sudan. Here, the economic plant is a short day plant, sorghum, and the general consensus is that it lacks traits associated with domestication; it may be cultivated, but is morphologically wild. Whatever its domestication/cultivation status, sorghum does not make an appearance as far north as modern day Egypt until the 8th century BC, at the site of Qasr Ibrim in lower Nubia (Deakin et al., 1998). By this time, there is another short day cereal recorded at the same site, originating from much further afield. *Panicum miliceum* or broomcorn millet was domesticated in North China, but forms and remains part of the Qasr Ibrim crop repertoire for several centuries (Clapham and Rowley-Conwy, 2007).

Not surprisingly, the irrigation-based societies of Bronze Age Mesopotamia also rely primarily on Southwest Asian domesticates, again emmer wheat and barley. Here too, the North China domesticated broomcorn millet has been recorded, on the basis of phytolith evidence, from the mid-second millennium BC site of Khani Masi in Northern Iraq (Laugier et al., 2022).

It is in peninsular India that the most significant reception from other regions of short day crops is seen, alongside the more familiar reception of Southwest Asian long day crops. For the third and second millennia BC, Fuller (2005) lists a wide range of crop taxa assembled within farming systems, originating from Southwest Asia, Africa, China, and the Indian region itself, comprising sorghum, ten species of millets, and several pulse crops, oilseeds, gourds and cucumbers.

In Bronze Age China, a range of indigenous short day crops, including broomcorn and foxtail millet, rice and buckwheat are joined by elements of the Southwest Asian long day suite of crops, notably wheat and barley, by the third millennium BC (Liu et al., 2017).

In summary, agriculture in many regions of the Old World, prior to the third millennium BC, is characterized by crops being cultivated relatively close to their regions of origin, sometimes

displaying full morphological domestication, other times wild or intermediate forms. As well as being close to their ancestral region, they were typically cultivated close to their ancestrally optimal season. In other seasons, other forms of food acquisition are repeatedly attested including foraging, fishing and hunting. At various stages during the third and second millennia BC, the focus upon the cultivated field extends in time across the farming calendar. An enlargement of the annual cycle of crop cultivation is facilitated by the cultivation of crops far from their regions of origin. The translocation of long day plants is particularly amenable to management in societies that exert considerable control over water supplies. The addition of adaptable crops to such an anthropic system of multicropping are those that have, at some stage, acquired mutations in flowering-time genes that allow crops to flower later in the growing season (Liu et al., 2017, 2019).

MECHANISM OF SELECTION AND ITS UNINTENDED CONSEQUENCES

Views have varied upon how much domestication depended upon conscious or unconscious human action (e.g., Zohary, 2004; Abbo et al., 2012; Larson et al., 2014). Some models have envisaged the first farmers having something in common with more recent breeders, selecting and nurturing chosen traits from generation to generation. An example of this could be the selection of glutinous grains of rice (Fuller and Rowlands, 2011). Others have inferred from the very slow timescale of the fixation of observed domestication traits that unconscious selection would have played a more significant role than sentient choice. In the context of transition between brittle rachis and tough rachis forms, plausible arguments for both conscious (e.g., Tzarfati et al., 2013) and unconscious selection (e.g., Purugganan and Fuller, 2011) may be envisaged. However, the transition from photoperiod-sensitive to photoperiod-insensitive crops is far more likely to have resulted from unconscious selection. Translocation across continents did not invariably entail translocation across latitudes, but when it did, evidence shows that there was selection pressure in favor of forms that are photoperiod insensitive (Lister et al., 2009, 2018).

An analogy may be the 19th century introduction of Turkey Red Wheat to the High Plains of North America. The primary driver of wheat cultivation in Kansas and neighboring states was cultural; Turkey Red was the seedcorn that Mennonite immigrants brought from Russia in the 1870s with only limited knowledge of the environments to which they would arrive, and for a number of decades would farm. Scientific breeding would not come to these crops for another generation, so it was primarily the perseverance of the Mennonite settlers that established the crop, now ancestral to many important varieties within the North American wheat belt (Quisenberry and Reitz, 1974).

A similar perseverance in displaced environments could generate the selection pressure that might lead to photoperiod insensitive forms. Once established in crop populations, they

could be employed to extend the growing season of multi-cropping systems. The fixation of this photoperiod insensitivity trait had other unintended consequences. As well as allowing the cultivation of crops within a displaced season, it also allowed their cultivation within a displaced latitude, the axis upon which seasonality is most dependent. The archaeological and genetic evidence for barley illustrates this point.

Barley was domesticated in the Near East approximately 11,000 years ago. Wild barley is a short day plant and predominantly possesses the photoperiod responsive variant of the *Ppd-H1* gene. This is an adaptive advantage in the range of wild barley in the Near East, where summers are hot and dry (Jones et al., 2008). For example, Jones et al. (2008) demonstrated that the non-responsive form of the *Ppd-H1* gene originated in certain populations of wild barley, (*H. vulgare* subsp. *spontaneum*) and that the non-responsive form (*ppd-H1*, Group A) originated from wild barley, rather than one type evolving from the other as a result of mutation during dispersal of landraces in Europe. It is thus possible that mutations in other genes involved in flowering time could also be present in wild progenitor populations. Cultivated barley spread beyond the region of domestication and into Europe, reaching the Balkans by 6,000 BC, then spreading outwards *via* two principal routes, one *via* the loess soils of the Rhine and Danube river valleys, and into the North European Plain, and the other along the Mediterranean coast *via* Italy and the Iberian peninsula, and into northern Europe (Barker, 1985; Price, 2003). The dating evidence has been taken to indicate delays at certain localities along the spread of agriculture. Such a delay at the southern edge of the Scandinavian basin was possibly the longest; agriculture appeared to halt for a period of 500–1,000 years until 4000 BC before being adopted in Ireland, Britain, and Scandinavia (Bogucki, 2000). The northerly spread through Scandinavia was slow, reaching the far north by ca. 500 BC. Barley, one of the most adaptable cereals, could be cultivated within the Arctic Circle, at latitudes of up to 70° (Vorren, 2005). These delays in the spread of agriculture were may be due to the slow assimilation of agricultural practices by existing indigenous human populations, to the time taken for crops to adapt to novel environments, or some combination of both factors.

As agriculture spread into northerly latitudes, where summer drought was no longer a problem, flowering early in the season became maladaptive. A recessive *ppd-H1* allele, which switched off flowering in response to long days, prevailed in these northern climes (Jones et al., 2008), enabling spring-sown barley, over the long summer season, to build biomass before flowering. The prevalence of the insensitive *ppd-H1* allele increased as barley cultivation spread further north. This latitudinal cline observed amongst landrace accessions by Jones et al. (2008) is even more pronounced in material from historical accessions, which extend into the Arctic Circle (Lister et al., 2009). The authors of this study propose that the cline observed in historic material has been “overstamped” by more recent crop movements. The data in these two studies suggest that the switching off of this gene played a key role in the most northerly cereal cultivation of all.

CONCLUSION

Much of the focus within domestication studies has concerned stem morphology and its consequences for harvesting technique. There are other trait shifts in the evolution of people/plant relationships, also with significant impact upon those relationships, among which photoperiod response is a notable example. Just as evolutionary shifts in stem morphology were central to the shift from foraging to farming, so were subsequent evolutionary shifts in photoperiod response central, both to the emergence of complex hierarchical civilizations, but also to the spread of agriculture across the latitudinal range of the globe.

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