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OVERVIEW

From Crop Domestication to Super-domestication

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Research related to crop domestication has been transformed by technologies and discoveries in the genome sciences as well as information-related sciences that are providing new tools for bioinformatics and systems' biology. Rapid progress in archaeobotany and ethnobotany are also contributing new knowledge to understanding crop domestication. This sense of rapid progress is encapsulated in this Special Issue, which contains 18 papers by scientists in botanical, crop sciences and related disciplines on the topic of crop domestication. One paper focuses on current themes in the genetics of crop domestication across crops, whereas other papers have a crop or geographic focus. One feature of progress in the sciences related to crop domestication is the availability of well-characterized germplasm resources in the global network of genetic resources centres (genebanks). Germplasm in genebanks is providing research materials for understanding domestication as well as for plant breeding. In this review, we highlight current genetic themes related to crop domestication. Impressive progress in this field in recent years is transforming plant breeding into crop engineering to meet the human need for increased crop yield with the minimum environmental impact – we consider this to be 'super-domestication'. While the time scale of domestication of 10 000 years or less is a very short evolutionary time span, the details emerging of what has happened and what is happening provide a window to see where domestication might – and can – advance in the future.

Key words: Evolution, gene cloning, gene pyramiding, gene duplication, marker assisted selection, QTL, crop wild relatives.

INTRODUCTION

As human societies have evolved so have the plants in the human environment. The transition from gathering wild plants to cultivation involved increasing interaction between humans and the plants they used. The subsequent genetic changes in these plants resulting in domestication of some of these cultivated species reflect the genius of early farmers, who were the first plant breeders. The present generation of plant breeders has tools available that enable them to be plant engineers. In this article that overviews the topic and the range of papers in this Special Issue of *Annals of Botany* on crop domestication, we discuss current themes related to the genetics of crop domestication and crop genepools that are helping to accelerate the transition from plant breeding to plant engineering, from crop domestication to crop super-domestication.

Cultivated or domesticated plants, when mankind propagates, plants and harvests them, have played significant roles in many of the advances that pure and applied botanical sciences have made in the last few centuries. The earliest farmers recognized useful genetic variation that could be chosen from the wild, planted, harvested and reselected in order to gradually develop improved populations with a range of desirable traits. The domesticated forms bore only limited resemblance to their wild ancestors due to the selection of domestication genes. Early in the 18th century, the first conscious hybridization of plants occurred using the cultivated ornamental species *Dianthus* (Phillips, 2006). Knowledge of plant hybridization paved the way for the use by plant breeders of intra- and interspecific hybridization in crop improvement. Mendel's discovery of the laws of genetics, based most famously on his experiments with the domesticated garden pea, led to improved understanding of the variation in domesticated and wild species that so impressed Darwin (1859). Subsequently, sophisticated crop breeding programmes were developed that enabled more efficient introduction of desirable traits from one cultivar to another. Knowledge of the evolutionary relationships between crops and their wild progenitors has facilitated more efficient exploitation of the genetic resources represented by the wild relatives of domesticated species (for a review, see Hajjar and Hodgkin, 2007). Currently, domesticated crops such as rice, maize and tomato are major targets of studies in molecular genetics. Research on domestication-related traits is leading to a better understanding of how genetic control of phenotypic differences is effected. For example, in determining the extent to which similar (orthologous) genes are involved in producing similar phenotypes in distantly related species and working out how to transfer desirable genes between species that cannot be hybridized sexually, and then how to control the expression of the genes once they are transferred.

Hybridization and selection have both been involved in the origin of crops and the process of domestication since early

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times. Bread wheat, which is a hexaploid ($2n = 6x = 42$ chromosomes), arose through fortuitous hybridization between tetraploid wheat (*Triticum turgidum* ssp. *dicoccum*, $2n = 4x = 28$) and diploid goatgrass (*Aegilops tauschii*, $2n = 2x = 14$), a weed of early wheat fields. New groups of bananas and plantains developed when diploid domesticated bananas (genome AA) spread into the range of wild *Musa balbisiana* (genome BB), producing the AAB and ABB triploids (see Heslop-Harrison and Schwarzacher, 2007). Modern strawberries (*Fragaria* × *ananassa*) are a consequence of hybridization between North American *F. virginiana* and South American *F. chiloensis* when these hitherto geographically isolated species were cultivated in close proximity in European gardens (Bringhurst and Voth, 1984). Selection, both intentionally by humans (conscious selection) and as a result of environmental factors (natural or automatic selection) has, in most crops, established the traits associated with the domestication syndrome (Hammer, 1984). Weed species have co-evolved with crops and have been under similarly intense selection pressures. Weed control through agronomy and the better competitive ability of crops has been continuous over the 10 000 years of agriculture, but weeds still reduce yields and contaminate crops. In rice, changing agricultural practices is leading to the emergence of new weedy rice forms in the last decade (Cao *et al.*, 2006). Thus, as with the crops, weeds are also evolving rapidly under selection.

Analysis of the genetic, genomic and molecular basis of the traits selected by early farmers that constitute the domestication syndrome in crops, such as loss of seed shattering and increased organ size, has been a major focus of much recent research. Profound insights into traits associated with crop domestication have resulted from the technologies and discoveries that make DNA analysis and manipulation possible (for review see Phillips, 2006). These technologies are associated with PCR, development of transgenic crops and chromosome painting, as well as DNA sequencing and information processing. The rapid spread of communication technologies enable new knowledge to be disseminated at a remarkable speed worldwide and have ushered in global research initiatives related to crop genome analysis and related research. These tools have been used in various crops for the development of genome maps, QTL analysis, whole-genome sequencing, fine-resolution mapping and gene cloning. These scientific advances have also contributed to crop improvement, with the application of, for example, marker-assisted selection. The use of molecular techniques has provided a range of new insights into domestication and its future course.

FINE-RESOLUTION MAPPING AND GENE CLONING OF DOMESTICATION-RELATED GENES

Plants have relatively few morphological traits that are controlled by single genes with distinct alleles showing Mendelian segregation – Mendel was fortunate to find seven independent and non-interacting genes. The development of molecular markers to analyse directly DNA or gene products has meant that tens of thousands of segregating polymorphisms can be analysed in a species. This has made it possible to locate genes controlling both qualitative and quantitative characters very precisely within the genome, understand their interactions, and then to study the phenotypic effects of individual genes or small regions of chromosome in segregating populations (Paterson, 2002; Hancock, 2005; Zhang *et al.*, 2005). In a number of studies, quantitative trait loci (QTL) affecting different elements of the domestication syndrome are collocated to the same locus or the same small chromosomal region, suggesting either pleiotropy or close linkage of the gene(s) concerned. It can be difficult to distinguish pleiotropy from close linkage (Bomblies and Doebley, 2006) but in this Special Issue, Weeden (2007) gives some examples of pleiotropy in pea; other examples are discussed below.

Fine mapping of genes has led to the ability to clone domestication-related genes and unravel the molecular basis of domestication-related changes. For example, the two genes that are most important in relation to spikelet shattering in rice (*sh4* and *qSH1*) have been cloned (Konishi *et al.*, 2006; Li *et al.*, 2006; discussed by Sweeney and McCouch, 2007, in this Special Issue). *sh4* is the key shattering gene that distinguishes cultivated from wild rice, while the *qSH1* gene controls the difference in the degree of shattering between some indica and japonica varieties of rice. *sh4* is a transcription regulator and a single amino acid substitution results in reduced shattering. For *qSH1* a single nucleotide in the regulatory region of this gene results in the altered level of seed shattering. *sh4* activates the abscission process while *qSH1* regulates abscission-layer formation. Sequence analysis of *sh4* has revealed a single base-pair mutation that is responsible for non-shattering and this change is the same in both indica and japonica rice varieties (Lin *et al.*, 2007). This result raises doubts about whether Asian rice was domesticated more than once, as has been suggested in several recent papers (for a review see Sang and Ge, 2007). In contrast, sequencing and comparing seven loci in wild and landrace barley have provided strong evidence that barley was domesticated once in the Fertile Crescent and a second time between 1500 and 3000 km to the east (Morrell and Clegg, 2007). Analysis of domestication genes across diverse germplasm can resolve questions about where, from what and how many times a crop was domesticated.

Differences in nucleotide sequence and/or levels of transcription of different alleles of transcriptional regulators affect the phenotypes produced by target genes. In wheat, the *Q* gene is pleiotropic for many domestication traits. The wild-type allele *q* is associated with a fragile rachis and grain that does not thresh free of the chaff, whereas the domestication allele *Q* is associated with a tough rachis and free-threshing grain (Simons *et al.*, 2006). Comparison of the structure and activity of these two alleles suggests that *q* is transcribed at lower levels than *Q* and that the q protein functions less efficiently than the protein product of *Q* (Simons *et al.*, 2006). *Q* is not known in the wild progenitors of wheat, but human selection post-domestication seems to have resulted in up-regulation of *Q* such that *Q* has more than twice the effect of *q* (Simons *et al.*, 2006). Similarly, some of the differences in branching and spikelet suppression distinguishing domesticated maize from wild teosinte and controlled by *tb1* have been attributed to up-regulation of *tb1* in maize (Hubbard *et al.*, 2002). To date, most domestication genes that have been cloned are diverse transcription factors that are usually functional (Doebley *et al.*, 2006; Komatsuda *et al.*, 2007). Thus the role of human selection on wild populations during crop domestication at the gene level has been modification rather than elimination of gene function (Consonni *et al.*, 2005; Doebley *et al.*, 2006). This perhaps reflects the relative rarity of mutations leading to new structural or functional genes and the short time span of crop domestication.

DOMESTICATION TRAIT ALLELES CAN BE FOUND IN WILD POPULATIONS

Traits of the domestication syndrome such as loss of seed dispersal, loss of seed dormancy or loss of protection against herbivores are considered disadvantageous in wild plants (e.g. Crawley and Brown, 1995). These are often recessive alleles so their effects would be masked in the heterozygotes that make up the bulk of many wild populations. However, these recessive alleles become exposed through the inbreeding associated with domestication in many crops.

In maize, pleiotropic effects associated with *zfl2* are such that selection for increased yield via increases in row number controlled by *zfl2* would probably select also for earlier flowering and fewer ears placed lower on the plant (Bomblies and Doebley, 2006). This led Bomblies and Doebley (2006) to suggest that, in general, undesirable secondary effects associated with pleiotropic genes could limit selection for favourable ‘domestication alleles’ during early stages of the differentiation of a crop from its wild progenitor. On the other hand, selection for beneficial traits controlled by pleiotropic genes could result in associated neutral or even detrimental traits being concurrently selected. This may explain, at least partially, the presence, in wild populations, of alleles for traits of the domestication syndrome that apparently evolved prior to domestication and survived despite their possibly deleterious effects in the wild. Examples of this include alleles of the ‘hidden QTL’ *fw2·2* for increased fruit size in cultivated tomatoes (*Solanum lycopersicum*) that are also found in the wild cherry tomato (*S. lycopersicum* var. *cerasiforme*; Nesbitt and Tanksley, 2002; Bai and Lindhout, 2007). Alleles of the regulatory locus *CAULIFLOWER* (*BoCAL*) in *Brassica oleracea* that contribute to, but are insufficient to cause, development of abnormal inflorescence are present in moderate frequency in wild populations of *B. oleracea* subsp. *oleracea* (Purugganan *et al.*, 2000).

A key gene responsible for some differences between maize and its wild progenitor is the *teosinte branched 1* (*tb1*) mutant that has pleiotropic effects on apical dominance, length of lateral branches, growth of blades of leaves on lateral branches, and development of the pedicillate spikelet in the female inflorescence (Hubbard *et al.*, 2002). In the progenitor of maize, teosinte (*Zea mays* var. *parviglumis*), a *tb1* region haplotype with sequences identical to that of the major maize *tb1* haplotype was found. This result suggested that haplotypes that confer maize-like phenotypes could predate domestication (Clark *et al.*, 2004). Thus, the high-speed evolution represented by crop domestication can be the result of strong selection pressures on pre-existing variation.

Humans caused a major shift in the morphological traits of wild plants by selecting genes of both large effect and small effect to create crops with higher yield of desired product. In azuki bean (*Vigna angularis*) domestication has reduced seed yield on a per plant basis because farmers have selected determinate plants with larger pods and fewer large seeds per pod than its progenitor wild relative (A. Kaga, NIAS, Japan, unpubl. res.). Mathematical analysis of the functional and structural components of yield, including harvest index – a systems’ biology approach – have great potential to indicate future directions for selection (Guo *et al.*, 2006). The wild relatives of crops continue to be an important reservoir of genes for potential use in agriculture. Sometimes, the genes they have furnished have had a dramatic effect on yield, as shown by Tanksley and McCouch (1997) and by Cheng *et al.* (2007) in this Special Issue. Therefore, there is a continued urgency to conserve these wild genetic resources appropriately, both *in situ* and *ex situ*, and to characterize them for future crop improvement.

ORTHOLOGUES OF DOMESTICATION GENES AND THEIR ACTION

There are many different families of transcriptional regulators in plants and the transcriptional regulators involved in domestication discussed by Doebley *et al.* (2006) all belong to different families. Within a given family of transcriptional regulators, gene structure may be sufficiently conserved for similarities to be identified not just between genera of the same plant family but between taxonomically very distantly related species. Thus, *monoculm1* in maize shares similarities with *LATERAL SUPPRESSOR* from *Arabidopsis thaliana* and tomato (see Doust, 2007, in this Special Issue) and *Q* in wheat is similar to *APETALA2* (*AP2)* of *Arabidopsis* (Simons *et al.*, 2006). *AP2*-like genes appear to have a wide range of roles in plant development, but *Q* is so far the only *AP2*-like gene implicated in domestication (Simons *et al.*, 2006). One of the genes affecting shattering in rice, *qSH1*, may be an orthologue of *REPLUMLESS* (*RPL*) in *Arabidopsis* (Konishi *et al.*, 2006). *REPLUMLESS* is involved in formation of an abscission layer in the wall of the fruit, whereas *qSH1* affects formation of an abscission layer between pedicel and spikelet, but Konishi *et al.* (2006) suggest that this difference could be explained by differences in the transcriptional control of *RPL* and *qSH1.* The duplicate genes *zfl1* and *zfl2* of maize are orthologous to the *FLORICAULA/LEAFY* (*FLO/LFY*) genes of species of *Antirrhinum* and *Arabidopsis*, amongst others (Bomblies and Doebley, 2006). Among the various effects suggested for these genes is the change in phyllotaxy that produces whorled organs during flower development. In maize, *zfl2* is the candidate gene for a major effect QTL controlling the whorled versus two-ranked arrangement of female spikelets in maize versus teosinte. *FLO/LFY*-like genes have not been reported to affect inflorescence phyllotaxy in any other species, but Bomblies and Doebley (2006) suggest that a change in expression pattern could have allowed one of their orthologues to be annexed for a new role in maize.

Rice contains an orthologue of maize *tb1*, *OsTB1*, that, like maize *tb1*, affects lateral branching (Takeda *et al.*, 2003). Transgenic rice carrying an extra dose of *OsTB1* produced many fewer tillers than normal because of over-expression of *OsTB1*. A known mutant, *fine culm1* (*fc1*), with enhanced tiller production, mapped to the same locus as *OsTB1*, suggesting that *fc1* is an allele of *OsTB1*. Sequencing of *fc1* showed a deletion generating a premature stop codon, such that the predicted polypeptide product lacked the domain implicated in the DNA binding activity of the class of transcriptional regulators to which *tb1* belongs. Takeda *et al.* (2003) therefore suggest that alterations in the expression of *OsTB1* through dosage effects or use of mutants could be used to increase or decrease tiller number at will and thereby adapt rice morphology to differing agronomic situations (see also Doust, 2007, in this Special Issue).

In the major oilseed crop canola or oilseed rape (*Brassica juncea*, *B. napus* and *B. rapa*) losses of between 10–50 % of yield can occur due to unsynchronized pod shattering (Østergaard *et al.*, 2006) and require extensive management, including spraying with crop dessicants before harvest and windrowing before threshing. *Arabidopsis* has proved to be a useful model to study the phenomenon, where a transcriptional regulator, *FRUITFUL* (*FUL*), mediates pod dehiscence by inhibiting expression of genes controlling shattering. When this transcriptional regulator was introduced in *B. juncea* it was over-expressed and pods had no shattering. Further fine-tuning of the expression of this gene in canola may enable the required level of post-harvest shattering to be achieved (Østergaard *et al.*, 2006). Such intentional manipulations to fine-tune gene activity will certainly constitute super-domestication, where genetics interacts with crop management and agronomy.

Evidently much remains to be learned about the actions of transcriptional regulators and how they in turn are regulated. Recently, Clark *et al.* (2006) located a factor or factors controlling the levels of the message produced by the transcriptional regulator *teosinte branched 1* (*tb1*) in maize, and hence the phenotypic differences between maize and teosinte associated with *tb1*, to an intergenic region upstream from *tb1*. This region consists of a mixture of repetitive and unique sequences not previously considered to contribute to phenotypic variation. Doebley and Lukens (1998) had earlier proposed that modifications in *cis*-regulatory regions of transcriptional regulators would prove a predominant means for the evolution of novel forms, and the findings of Clark *et al.* (2006) appear to provide a supporting example. Plant-breeding-related companies are already looking at the effects of up- and downregulating all transcription factors in a given genome, aiming to learn more about the target genes of different transcription factors and producing a super-domesticate (Doebley *et al.*, 2006), perhaps with more success than gene mutation as a source of Dobzhansky's 'hopeful monsters'.

EFFECTS OF SELECTION ON DOMESTICATION GENES

Molecular techniques are not just enabling the position of domestication-related genes to be resolved but they can provide information on the effects of selection and number of generations required for domestication. By studying nucleotide polymorphism in different accessions of a crop upstream and downstream from domestication-related genes, it is possible to determine the extent to which selection is acting across the genome, the selective sweep (Clark *et al.*, 2004). Positive directional selection leads to reduced variation and linkage disequilibria in the respective regions (Palaisa *et al.*, 2004). By comparing sequence diversity around a domestication gene in the crop and its progenitor, a new view of the processes that sculptured the formation of the crops species can be attained. By analysis of nucleotide polymorphism around the *teosinte branched 1* (*tb1*) gene in a wide variety of maize accessions, it was found that human selection acted on the gene's regulatory region and was not detected in the protein-coding region (Wang *et al.*, 1999; Clark *et al.*, 2004). This was considered to be a consequence of the high rates of recombination in maize. From the analysis it was estimated that the time taken to domesticate maize was between 315–1023 years (Wang *et al.*, 1999). Studies of wheat remains at archaeological sites in southern Turkey and Syria, where wheat domestication is believed to have occurred, reveal a gradual change from dehiscent to indehiscent spikelets, suggesting indehiscence took over one millennium to become established (Tanno and Wilcox, 2006). Archaeological remains of rice from the lower Yangtze river suggests that rice domestication was a slow process (see Fuller, 2007, in this Special Issue) and this is supported by the wild-rice harvesting methods used today, which do not provide a selection pressure for non-shattering spikelets (Fig. 1). Both molecular and archaeobotanical studies suggest a long period of gathering and cultivation preceded domestication for these cereals. While domestication represents rapid change in evolutionary terms, in cereals the transition in the suite of characters that changed wild populations into domesticated crops took place over many centuries or millennia.

During domestication, population genetic diversity is reduced as a consequence of selection. Domestication-related genes experience a more severe genetic bottleneck due to selection than neutral genes, as discussed by Doebley *et al.*, (2006) and in this Special Issue by Yamasaki *et al.* (2007). Estimates of the severity of the genetic bottleneck of domestication based on comparison of genetic diversity found in their wild ancestors vary considerably from about 80 % in maize (Wright and Gaut, 2005), to 40–50 % in sunflower (Liu and Burke, 2006) and as little as 10–20 % in rice (Zhu *et al.*, 2007). Polyploid wheats have suffered two bottlenecks associated

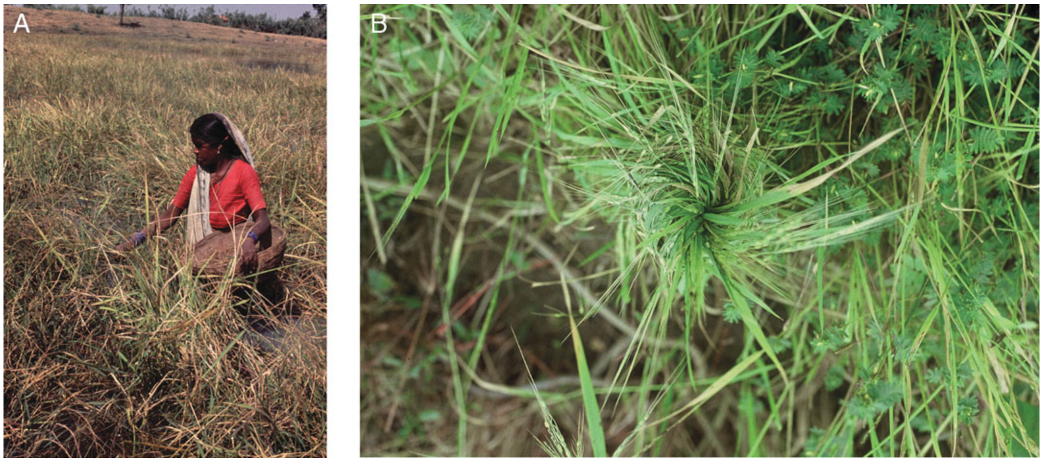

FIG. 1. Alternative contemporary ways of harvesting wild rice in India. (A) Beating panicles over a basket, and (B) twisting leaves and stem into bundles that collect shattered grain. These methods, plus swinging a basket over ripening panicles, are used to harvest wild rice in South Asia and West Africa (Oka, 1988).

with the transition from wild wheat and also due to polyploidy. Thus, hexaploid bread wheat has about 7 % and 30 % of the nucleotide diversity of its D and A/B genome donors, respectively (Dubcovsky and Dvorak, 2007). Determining how much diversity is lost during the genetic bottleneck of domestication can suggest approaches to future crop improvement, such as tapping high diversity gene sources in wild progenitors (Whitt *et al.*, 2002) or transgenic alteration of expression of selected genes (see Yamasaki *et al.*, 2007, in this Special Issue).

Detection of previously undetected domestication-related genes has become possible using QTL analysis and selective sweeps across the genome (Yamasaki *et al.*, 2007). This enables hidden domestication genes to be detected based on the selection profile of comparative sequences. Genomic comparison of crops and their wild progenitors for hidden domestication-related genomic regions is a new approach to detecting potentially useful diversity in wild progenitors for crop improvement.

GENE EVOLUTION

Genome sequencing has enabled the evolution of domestication-related genes to be elucidated. The wild and domesticated wheat species provide an example. The different domesticated wheat cultigens (cultivated species) evolved from hybridization events between wild and cultivated species (to form *Triticum aestivum* subsp. *spelta*) or selections from either wild (*T. monococcum* subsp. *monococcum* and *T. turgidum* subsp. *dicoccum*) or domesticated species (*T. aestivum* and *T. turgidum* subsp. *durum*). In this wild–domesticated polyploid series the grain-hardness locus (*Ha*) of wheat encodes friabilins that are composed of three proteins. The genes *Pina*, *Pinb* and *Gsp*-1 at the *Ha* locus encode these three proteins. Two of these genes, *Pina* and *Pinb*, were eliminated from both the A and B genomes of wheat after polyploidization into the tetraploid *T. turgidum*. In the hexaploid, *T. aestivum*, *Pina* and *Pinb* are present coming from the D genome donor, *Aegilops tauschii*. Comparison of the *Ha* locus in the same genome in diploid, tetraploid and hexaploid *Triticum* and *Aegilops* species revealed numerous genomic rearrangements, such as transposable element insertions, genomic deletions, duplications and inversions (Chantret *et al.*, 2005). Genomic rearrangements at the *Ha* locus were believed to be mainly caused by illegitimate recombination, where DNA sequences not originally attached to one another become joined, and this type of recombination is considered a major evolutionary mechanism in wheat species (Chantret *et al.* 2005). The complex evolution of the *H*a locus in wheat reflects the remarkably high rate of DNA replacement in wheat genes (Dubcovsky and Dvorak, 2007).

GENE AND GENOME DUPLICATION

An area where DNA technologies have had a particular impact on our understanding of domestication has been in relation to gene and genome duplication. As well as polyploidy, gene duplication is a common evolutionary phenomenon in plants (for review see Moore and Purugganan, 2005). In maize it has been estimated that about a third of genes are tandem duplicates due to unequal recombination or transposition events that have involved gene fragments (Emrich *et al.*, 2007). Rondeau *et al.* (2005) have shown duplication and subsequent functional specialization of NADH-MDH genes in some, but not all, grasses with C_4 photosynthesis. Among duplicated genes are a class called *n*early *i*dentical *p*aralogs (NIPs) that appear to be of recent origin. This class of duplicate gene shares $\geq$98 % identity. Many NIPs in maize are differentially expressed. This has lead to the suggestion that the variation in this class of duplicate gene provides new variation that may have had a selective advantage during domestication and improvement of maize (Emrich *et al.*, 2007), and again modelling of plant architecture may suggest routes for crop improvement (Guo *et al.*, 2006).

Reflecting the abundance of polyploids in the plant kingdom, many important crops exhibit both allopolyploidy (e.g. wheat, canola, tobacco, peanut and cotton) and autopolyploidy (e.g. watermelon, strawberries, potato and alfalfa). Allopolyploidy results in increased allelic diversity while autopolyploidy results in increased allelic copy number, both of which can lead to novel phenotypes. Since polyploidy is so common in plants they must have some selective advantages. Among the presumed main advantages of polyploidy are fixation of heterosis, duplication enabling evolution of gene function, and alteration of regulation.

The allopolyploid oilseed crop *Brassica napus* (canola) provides an example of how heterozygosity resulting from polyploidy can affect evolutionarily important traits. *Brassica napus* is thought to be derived from crosses between *B. oleracea* ($2n = 18$, CC genome) and *B. rapa* ($2n = 20$, AA genome). Using molecular markers, lines in mapping populations were compared at a transposition site with QTL for seed yield (Osborn *et al.* 2003*a*, Quijada *et al.*, 2006, Udall *et al.*, 2006). When the allelic arrangement was similar to that of the parental genotypes, *B. oleracea* and *B. rapa*, seed yields were lower. However, when the arrangement of alleles differed from these parental genotypes seed yields were higher. The best explanation for the results of these studies was that intergenomic heterozygosity increased seed yield in *B. napus*.

In allopolyploid cotton, an ancient polyploidy, it has been shown that some homoeologous genes are assigned to different (sub)functions, with gene expression compartmentalized to different tissue types and gene expression biased between homoeologs (Adams *et al.*, 2003, 2004). Thus, between the genomes of cotton, expression of homoeologous genes is developmentally regulated. It has been suggested that this may provide allopolyploids with greater plasticity in response to stress (Udall and Wendel, 2006). Further understanding of what causes changes in homoeologous gene function may provide avenues to manipulate gene expression.

Gene expression is generally dependent on hierarchically organized networks of regulators. The number of these regulators can be increased several-fold in polyploids and the overall consequences of polyploidy on gene expression at the end of regulatory networks are difficult to predict (Osborn *et al.*, 2003*b*). In a genome-wide analysis of synthetic allotetraploids between *Arabidopsis thaliana* and *A. arenosa*, about 5 % of genes showed divergence from the mid-parent value, suggesting non-additive gene regulation (Wang *et al.*, 2006*b*). For example, time of flowering in this synthetic allopolyploid was later than both parents. This was found to be the result of the epistatic interactions between two loci, one for flowering from *A. thaliana* (*FLC*) and the other from *A. arenosa* (*FRI*), that enhances *FLC* expression and inhibits flowering (Wang *et al.*, 2006*a*). In hexaploid wheat, latitude of breeding has influenced the selection of genes affecting earliness of flowering, but there is still much genetic diversity relating to both photoperiod and vernalization requirements of the selections (Goldringer *et al.*, 2006). The rapid reprogramming of biological pathways on polyploidization leads to novel variation that may be exploited by plant breeders.

Many breeding programmes involve wide and distant hybridization. These procedures cause dramatic genome change, sometimes leading to unpredictable results. Studies of ancient and modern polyploids provide a means of elucidating the effects of dramatic genome change on gene expression and regulation. Results from such studies should enable breeding programs to achieve the desired results.

ACHIEVING NEW LEVELS OF CROP YIELD AND NEW USES FOR CROPS

The future course of domestication will continue to rely on changes to the architecture, metabolism and physiology of crops. To reach new levels of crop yield and new uses for crops, a combination of applied and also theoretical approaches involving computer or systems' biology models will be required. To cope with new challenges to crop production, efficient approaches to screen germplasm for genes to both biotic and abiotic stresses in wild and cultivated germplasm are needed. Crops primarily used for food are now also being used to meet demands for sustainable fuel supply, while the use of plants for construction timbers and fibres in paper, textiles and composite products continues to increase. To provide value-added crops, new products from crops are being developed. Specialized plant products for processing (such as starches, oils, even plastics) for food, pharmaceutical, cosmetic and industrial uses are required for growing markets (Heslop-Harrison, 2002).

As information accumulates on domestication-related traits and their genome distribution, new avenues to attain higher yield and to tailor-make crops are opened up. Analysis of yield and plant height in a cross between two Japanese rice varieties, 'Koshihikari' and 'Habataki', revealed several QTLs for each trait. One QTL, *Gn1a*, increased grain productivity and acts by altering the production of the enzyme cytokinin oxidase/dehydrogenase that degrades the phytohormone cytokinin. By reducing the expression of *Gn1a*, cytokinin accumulates in inflorescence meristems, resulting in an increased number of grains and, hence, a plant with the potential for increased yield (Ashikari *et al.*, 2005). By accumulating a variety of yield-related QTLs for increasing both source to produce photosynthate and sink to accept photosynthate, new levels of yield may be achieved.

Throughout history, plants have been subjected to changing climate, and farmers have adopted new species and varieties to meet the challenges; indeed, post-glacial climate changes may have been one of the factors leading to the origin of agriculture and plant domestication. Climate change is affecting agriculture in the 21st century; some changes will be met within existing adaptations of plants, but other factors such as increased UV and carbon dioxide levels require new selections based on understanding of plant responses. Hidema and Kumagai (2006) reported considerable variation in UVB sensitivity of rice cultivars, which was caused by differences of one or two bases in the CPD (cyclobutane pyrimidine dimer) photolyase, altering the activity of the enzyme. They suggest that the resistance of rice to UVB radiation can therefore be increased by selective breeding or bioengineering of the genes encoding CPD photolyase. Although carbon dioxide enhancement is regularly used to improve glasshouse production, it is not clear how field crops will respond to changes in atmospheric carbon dioxide concentrations, involving complex interactions of phytosythesis with light and dark respiration (Bunce, 2005).

There is no naturally occurring waxy wheat variety but in bread wheat there are waxy loci in each of its three different genomes, A, B and D. The waxy locus encodes starch granule protein 1 (SGP-1). Different isoforms are encoded by genes in each genome (*sgpA1*, *sgpB1* and *sgpD1*). In the germplasm collection of bread wheat, cultivars lacking one of the three isoforms were found, two cultivars from Korea lacked SGP-A1, one from Japan lacked SPG-B1 and one from Turkey lacked SPG-D1. By making appropriate crosses, these genes were combined in a single plant, resulting in the first waxy wheat, which had a null for all three isoforms of SGP-1 (Yamamori *et al.*, 2000), an example of using markers for identification of alleles and then marker-assisted selection to find the desired allele combination. The effort to produce waxy wheat in Japan has led to its use as an ingredient for improved Japanese-style noodles. These examples show the value of screening germplasm collections with diverse material for useful genetic variation, but also emphasize that it is not always necessary to search in exotic material or employ radical techniques to make innovative progress in plant breeding.

SUPER-DOMESTICATION

We are entering a new era in relation to human understanding of and influence on the genetics of crop domestication. Current research on genes related to crop domestication is providing pieces in the complex jigsaw of gene evolution (see also Hancock, 2005), networking, regulation and expression in our most important plants. Introduction of alien genes through transgenic technology may be difficult (King *et al.*, 2004), but continued advances in crop improvement will depend on understanding the genome and its genes.

Super-domesticates can be constructed with knowledge-led approaches using the range of current technologies. Here, we use the term super-domestication to refer to the processes that lead to a domesticate with dramatically increased yield that could not be selected in natural environments from naturally occurring variation without recourse to new technologies. The array of genome manipulations that have been developed, mainly since the 1980s, enable barriers to gene exchange to be overcome and have lead to super-domesticates with dramatically increased yields, resistances to biotic and abiotic stresses, and with new characters for the marketplace. Hybrid rice (see Cheng *et al.*, 2007, in this Special Issue) can be considered a super-domesticate.

The teams of scientists that support plant breeders are planning and conducting research to change crops radically. For example, changing crops from C_3 photosynthesis to C_4 photosynthesis is being proposed because it is now known that plants with C_3 photosynthesis have enzymes for C_4 photosynthesis, and even well-developed C_4 pathways can be found at certain locations in C_3 plants. In addition, C_4-enzyme genes have been inserted into and successfully expressed in rice (Mitchell and Sheehy, 2006). Conversion of a crop from C_3 to C_4 photosynthesis would certainly be a super-domesticate.

It was with this background of rapid progress being made in studies of crop domestication that a meeting was organized in Tsukuba, Japan, in October 2006, by the National Institute of Agrobiological Sciences (NIAS) and the Organisation for Economic Cooperation and Development (OECD) and supported by *Annals of Botany*. While the Tsukuba meeting was being planned, a different meeting, entitled *Plants, People and Evolution*, sponsored by the Linnean Society of London, the Systematics Association and *Annals of Botany* was in preparation. This meeting was held in London in August 2006. Selected papers from these meetings appear in this Special Issue of *Annals of Botany*.

Progress in understanding crop domestication, and further advances that lead to greater quantities and improved quality of food crops, depend increasingly on multidisciplinary team approaches (Zeder *et al.*, 2006; Wuchty *et al.*, 2007). Scientists representing a diversity of botanical and crop-science backgrounds, archaeobotanists, crop evolutionary biologists, geneticists, ethnobotanists, plant breeders, statisticians and biotechnology specialists contribute papers in this present volume. The papers include both reviews of topics related to crop domestication and original research articles. Two key papers discuss domestication in the New World (Pickersgill, 2007) and the Old World (Fuller, 2007), while the papers that follow relate to particular crops or groups of crops. Included are papers on crops that have been intensively studied by molecular methods, e.g. maize (Yamasaki *et al.*, 2007), barley (Azhaguvel and Komatsuda, 2007; Pourkheirandish and Komatsuda, 2007), tomato (Bai and Lindhout, 2007), wheat (Waines and Ehdaie, 2007); some whose genomes have been completely sequenced, e.g. rice (Cheng *et al.*, 2007; Sweeney and McCouch, 2007) and sorghum (Dillon *et al.*, 2007), or where sequencing projects are proceeding actively, e.g. soybean (Liu *et al.*, 2007) and common bean (*Phaseolus vulgaris*; Papa *et al.*, 2007), and some where domestication is still at an early stage, e.g. giant cacti (Casas *et al.*, 2007), artichoke (Sonnante *et al.*, 2007) or banana (Heslop-Harrison and Schwarzacher, 2007). Scientists working on minor crops envy the amount of information being rapidly accumulated on model crops, but by extrapolation information from model species and model crops is already hastening advances in minor crops. This will be particularly true for current genomic initiatives in closely related crops such as the legumes (Weeden, 2007), where data from common bean and soybean will benefit the closely related African and Asian *Vigna* (Isemura *et al.*, 2007). Knowledge of the sorghum genome can be tapped to make progress in understanding the complex genome of sugarcane (Dillon *et al.*, 2007) and that of the rice genome for banana (Heslop-Harrison and Schwarzacher, 2007).

Minor crops, by the very fact that less is known about them, provide the potential of rapidly finding new insights into crop domestication (e.g. Fukunaga *et al.*, 2006).

The papers in this Special Issue are appearing in an area where there is currently much scientific progress. It is hoped that the papers here will stimulate ideas to help sciences associated with crop domestication achieve needed future super-domesticates.

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LITERATURE CITED

Adams KL, Cronn R, Percifield R, Wendel JF. 2003. Genes duplicated by polyploidy show unequal contribution to the transcriptome and organ-specific reciprocal silencing. *Proceedings of the National Academy of Sciences USA* **100**: 4649–4654.

Adams KL, Percifield R, Wendel JF. 2004. Organ-specific silencing of duplicated genes in a newly synthesized cotton allotetraploid. *Genetics* **168**: 2217–2226.

Ashikari M, Sakakibara H, Lin S, Yamamoto T, Takashi T Nishimura A, *et al.* 2005.Cytokinin oxidase regulates rice grain production. *Science* **309**: 741–745.

Azhaguvel P, Komatsuda T. 2007. A phylogenetic analysis based on nucleotide sequence of a marker linked to the brittle rachis locus indicates a diphyletic origin of barley. *Annals of Botany* **100**: 1009–1015.

Bai Y, Lindhout P. 2007. Domestication and breeding of tomatoes: what have we gained and what can we gain in the future? *Annals of Botany* **100**: 1085–1094.

Bomblies K, Doebley JF. 2006. Pleiotropic effects of the duplicate maize *FLORICAULA/LEAFY* genes *zfl1* and *zfl2* on traits under selection during maize domestication. *Genetics* **172**: 519–531.

Bringhurst RS, Voth V. 1984. Breeding octoploid strawberries. *Iowa State Journal of Research* **58**: 371–381.

Bunce JA. 2005. Response of respiration of soybean leaves grown at ambient and elevated carbon dioxide concentrations to day-to-day variation in light and temperature under field conditions. *Annals of Botany* **95**: 1059–1066.

Cao Q, Lu B-R, Xia H, Rong J, Sala F, Spada A, Grassi F. 2006. Genetic diversity and origin of weedy rice (*Oryza sativa* f. *spontanea*) populations found in north-eastern China revealed by simple sequence repeat (SSR) markers. *Annals of Botany* **98**: 1241–1252.

Casas A, Otero-Arnaiz A, Pérez-Negrón E, Valiente-Banuet A. 2007. *In situ* management and domestication of plants in Mesoamerica. *Annals of Botany* **100**: 1101–1115.

Chantret N, Salse J, Sabot F, Rahman S, Bellec A, Laubin B, Dubois I, Dossat C, *et al.* 2005. Molecular basis of evolutionary events that shaped the *Hardness* locus in diploid and polyploid wheat species (*Triticum* and *Aegilops*). *The Plant Cell* **17**: 1033–1045.

Cheng S-H, Zhuang J-Y, Fan Y-Y, Du J-H, Cao L-Y. 2007. Progress in research and development in hybrid rice: a super-domesticate in China. *Annals of Botany* **100**: 959–966.

Clark RM, Linton E, Messing J, Doebley JF. 2004. Pattern of diversity in the genomic region near the maize domestication gene *tb1*. *Proceedings of the National Academy of Sciences USA* **101**: 700–707.

Clark RM, Wagler TN, Quijada P, Doebley J. 2006. A distant upstream enhancer at the maize domestication gene *tb1 has* pleiotropic effects on plant and inflorescent architecture. *Nature Genetics* **38**: 594–597.

Consonni G, Gavazzi G, Dolfini S. 2005. Genetic analysis as a tool to investigate the molecular mechanisms underlying seed development in maize. *Annals of Botany* **96**: 353–362.

Crawley MJ, Brown SL. 1995. Seed limitation and the dynamics of feral oilseed rape on the M25 motorway. *Proceedings of the Royal Society of London Series B* **259**: 49–54.

Darwin C. 1859. *The origin of species by natural selection or the preservation of favoured races in the struggle for life*, 1st edn. London: John Murray.

Dillon SL, Shapter FM, Henry RJ, Cordeiro G, Izquierdo L, Lee SL. 2007. Domestication to crop improvement: genetic resources for *Sorghum* and *Saccharum* (Andropogoneae). *Annals of Botany* **100**: 975–989.

Doebley J, Lukens L. 1998. Transcriptional regulators and the evolution of plant form. *The Plant Cell* **10**: 1075–1082.

Doebley J, Gaut BS, Smith BD. 2006. The molecular genetics of crop domestication. *Cell* **127**: 1309–1321.

Doust A. 2007. Architectural evolution and its implications for domestication in grasses. *Annals of Botany* **100**: 941–950.

Dubcovsky J, Dvorak J. 2007. Genome plasticity: a key factor in the success of polyploid wheat under domestication. *Science* **316**: 1862–1866.

Emrich SJ, Li L, Wen T-J, Yandeau-Nelson MD, Fu Y, Guo L, *et al.* 2007. Nearly identical paralogs: implications for maize (*Zea mays* L.) genome evolution. *Genetics* **175**: 429–439.

Fukunaga K, Ichitani K, Kawase M. 2006. Phylogenetic analysis of the rDNA intergenic spacer subrepeats and its implications for the domestication history of foxtail millets, *Setaria italica. Theoretical and Applied Genetics* **113**: 261–269.

Fuller DQ. 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. *Annals of Botany* **100**: 903–924.

Goldringer I, Prouin C, Rousset M, Galic N, Bonnin I. 2006. Rapid differentiation of experimental populations of wheat for heading time in response to local climatic conditions. *Annals of Botany* **98**: 805–817.

Guo Y, Ma Y, Zhan Z, Li B, Dingkuhn M, Luquet D, De Reffye P. 2006. Parameter optimization and field validation of the functional–structural model GREENLAB for maize. *Annals of Botany* **97**: 217–230.

Hajjar R, Hodgkin T. 2007. The use of wild relatives in crop improvement: a survey of developments over the last 20 years. *Euphytica* **156**: 1–13.

Hammer K. 1984. Das Domestikationssyndrom. *Kulturpflanze* **32**: 11–34.

Hancock JF. 2005. Contributions of domesticated plant studies to our understanding of plant evolution. *Annals of Botany* **96**: 953–963.

Heslop-Harrison JS. 2002. Exploiting novel germplasm. *Australian Journal of Agricultural Research* **53**: 1–7.

Heslop-Harrison JS, Schwarzacher T. 2007. Domestication, genomics and the future for banana. *Annals of Botany* **100**: 1073–1084.

Hidema J, Kumagai T. 2006. Sensitivity of rice to ultraviolet-B radiation. *Annals of Botany* **97**: 933–942.

Hubbard L, McSteen P, Doebley J, Hake S. 2002. Expression patterns and mutant phenotype of *teosinte branched1* correlate with growth suppression in maize and teosinte. *Genetics* **162**: 1927–1935.

Isemura T, Kaga A, Konishi S, Ando T, Tomooka N, Han OK, Vaughan DA. 2007. Genome dissection of traits related to domestication in azuki bean (*Vigna angularis*) and comparison with other warm-season legumes. *Annals of Botany* **100**: 1053–1071.

King D, Dalton H, Heslop-Harrison JS. 2004., and 25 others. *GM Science Review. Second Report. An open review of the science relevant to GM crops and food based on interests and concerns of the public.* London: HMSO. http://www.gmsciencedebate.org.uk/report/pdf/gmsci-report2-full.pdf. Accessed June 2007.

Komatsuda T, Pourkheirandish M, He C, Azhaguvel P, Kanamori H, Perovic D, *et al.* 2007. Six-rowed barley originated from a mutation in a homeodomain-leucine zipper 1-class homeobox gene. *Proceedings of the National Academy of Sciences USA* **104**: 1424–1429.

Konishi S, Izawa T, Lin S-Y, Ebana K, Fukuta Y, Sasaki T, Yano M. 2006. An SNP caused loss of seed shattering during rice domestication. *Science* **312**: 1392–1396.

Li C, Zhou A, Sang T. 2006. Rice domestication by reduced shattering. *Science* **311**: 1936–1939.

Lin Z, Griffith ME, Li X, Zhu Z, Tan L, Fu Y, Zhang W, Wang X Xie D, Sun C. 2007. Origin of seed shattering in rice (*Oryza sativa* L.) *Planta* **226**: 11–20.

Liu A, Burke JM. 2006. Patterns of nucleotide diversity in wild and cultivated sunflowers. *Genetics* **173**: 321–330.

Liu B, Fujita T, Yan Z-H, Sakamoto S, Xu D, Abe J. 2007. QTL mapping of domestication related traits in soybean (*Glycine max*). *Annals of Botany* **100**: 1027–1038.

Mitchell PL, Sheehy JE. 2006. Supercharging rice photosynthesis to increase yield. *New Phytologist* **171**: 688–693.

Moore RC, Purugganan MD. 2005. The evolutionary dynamics of plant duplicate genes. *Current Opinion in Plant Biology* **8**: 122–128.

Morrell PL, Clegg MT. 2007. Genetic evidence for a second domestication of barley (*Hordeum vulgare*) east of the Fertile Crescent. *Proceedings of the National Academy of Sciences USA*. **104**: 3289–3294.

Nesbitt TC, Tanksley SD. 2002. Comparative sequencing in the genus *Lycopersicon:* implications for the evolution of fruit size in the domestication of cultivated tomatoes. *Genetics* **162**: 365–379.

Oka HI. 1988. *Origin of cultivated rice*. Amsterdam: Elsevier.

Osborn TC, Butrulle DV, Sharpe AG, Pickering KJ, Parkin IAP, Parker JS, Lydiate DJ. 2003*a*. Detection and effects of a homeologous reciprocal transpostion in *Brassica napus. Genetics* **165.**: 1569–1577.

Osborn TC, Pires JC, Birchler JA, Auger DL, Chen ZJ, Lee HS, *et al.* 2003*b*. Understanding mechanisms of novel gene expression in polyploids. *Trends in Genetics* **19**: 141–147.

Østergaard L, Kempin SA, Bies D, Klee HJ, Yanofsky MF. 2006. Pod shatter-resistant *Brassica* fruit produced by ecotopic expression of the *FRUITFULL* gene. *Plant Biotechnology Journal* **4**: 45–51.

Palaisa K, Morgante M, Tingey S, Rafalski A. 2004. Long-range patterns of diversity and linkage disequilibrium surrounding the maize *Y1* gene are indicative of an asymmetric selective sweep. *Proceedings of the National Academy of Sciences USA* **101**: 9885–9890.

Papa R, Bellucci E, Rossi M, Leonardi S, Rau D, Gepts P, Nanni L, Attene G. 2007. Tagging the signatures of domestication in common bean (*Phaseolus vulgaris*) by means of pooled DNA samples. *Annals of Botany* **100**: 1039–1051.

Paterson AH. 2002. What has QTL mapping taught us about plant domestication? *New Phytologist* **154**: 591–608.

Phillips RL. 2006. Genetic tools from nature and the nature of genetic tools. *Crop Science* **46**: 2245–2252.

Pickersgill B. 2007. Domestication of plants in the Americas: insights from Mendelian and molecular genetics. *Annals of Botany* **100**: 925–940.

Pourkheirandish M, Komatsuda T. 2007. The importance of barley genetics and domestication in a global perspective. *Annals of Botany* **100**: 999–1008.

Purugganan MD, Boyles AL, Suddith JI. 2000. Variation and selection at the *CAULIFLOWER* floral homeotic gene accompanying the evolution of domesticated *Brassica oleracea*. *Genetics* **155**: 855–862.

Quijada PA, Udall JA, Lambert B, Osborn TC. 2006. Quantitative trait analysis of seed yield and other complex traits in hybrid spring rapeseed (*Brassica napus* L.). 1. Identification of genomic regions from winter germplasm. *Theoretical and Applied Genetics* **113**: 549–561.

Rondeau P, Rouch C, Besnard G. 2005. NADP-malate dehydrogenase gene evolution in Andropogoneae (Poaceae): gene duplication followed by sub-functionalization. *Annals of Botany* **96**: 1307–1314.

Sang T, Ge S. 2007. The puzzle of rice domestication. *Journal of Integrative Plant Biology* **49**: 760–768.

Simons KJ, Fellers JP, Trick HN, Zhang Z, Tai Y-S, Gill BS, Faris JD. 2006. Molecular characterization of the major wheat domestication gene *Q*. *Genetics* **172**: 547–555.

Sonnante G, Pignone D, Hammer K. 2007. The domestication of artichoke and cardoon: from Roman times to the genomic age. *Annals of Botany* **100**: 1095–1100.

Sweeney M, McCouch S. 2007. The complex history of the domestication of rice. *Annals of Botany* **100**: 951–957.

Takeda T, Suwa Y, Suzuki M, Kitano H, Ueguchi-Tanaka M, Ashikari M, Matsuoka M, Ueguchi C. 2003. The *OsTB1* gene negatively regulates lateral branching in rice. *The Plant Journal* **33.**: 513–520.

Tanksley SD, McCouch SR. 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* **277**: 1063–1066.

Tanno K, Wilcox G. 2006. How fast was wild wheat domesticated? *Science* **311**: 1886.

Udall JA, Wendel JF. 2006. Polyploidy and crop improvement. *Crop Science* **46**(S1): 3–14.

Udall JA, Quijada PA, Lambert B, Osborn TC. 2006. Quantitative trait analysis of seed yield and other complex traits in hybrid spring rapeseed (*Brassica napus* L.). 2. Identification of alleles from unadapted germplasm. *Theoretical and Applied Genetics* **113**: 597–609.

Waines JG, Ehdaie B. 2007. Domestication and crop physiology: roots of green-revolution wheat. *Annals of Botany* **100**: 991–998.

Wang J, Tian L. Lee HS, Chen ZJ. 2006*a*. Nonadditive regulation of *FRI* and *FRC* loci meditates flowering-time variation in *Arabidopsis* allopolyploids. *Genetics* **173**: 965–974.

Wang J, Tian L. Lee HS, Wei NE, Jiang H, Watson B, *et al.* 2006*b*. Genomewide nonadditive gene regulation in *Arabidopsis* allotetraploids. *Genetics* **172**: 507–517.

Wang R-L, Stec A, Hey J, Lukens L, Doebley J. 1999. The limits of selection during maize domestication. *Nature* **398**: 236–239.

Weeden NF. 2007. Genetic changes accompanying the domestication of *Pisum sativum*: is there a common genetic basis to the 'domestication syndrome' for legumes? *Annals of Botany*: **100**: 1017–1025.

Whitt SR, Wilson LM, Tenaillon MI, Gaut BS, Buckler IV ES. 2002. Genetic diversity and selection in the maize starch pathway. *Proceedings of the National Academy of Sciences USA* **99**: 12959–12962.

Wright SI, Gaut BS. 2005. Molecular population genetics and the search for adaptive evolution in plants. *Molecular Biology and Evolution* **22**: 506–519.

Wuchty S, Jones BJ, Uzzi B. 2007. The increasing dominance of teams in production of knowledge. *Science* **316**: 1036–1039.

Yamamori M, Fujita S, Hayakawa K, Matsuki J, Yasui T. 2000. Genetic elimination of a starch granule protein, SGP-1, of wheat generates an altered starch with apparent high amylose. *Theoretical and Applied Genetics* **101**: 21–29.

Yamasaki M, Wright SI, McMullen MD. 2007. Genomic screening for artificial selection during domestication and improvement in maize. *Annals of Botany* **100**: 967–973.

Zeder MA, Bradley DG, Emshwiller E, Smith BD., eds. **2006.** *Documenting domestication: new genetic and archaeological paradigms.* Berkeley, CA: University of California Press.

Zhang ZH, Qu X, Wan S, Chen Sh, Zhu Y. 2005. Comparison of QTL controlling seedling vigour under different temperature conditions using recombinant inbred lines in rice (*Oryza sativa*). *Annals of Botany* **95**: 423–429.

Zhu Q, Zheng X, Luo J, Gaut BS, Ge S. 2007. Multilocus analysis of nucleotide variation of *Oryza sativa* and its wild relatives: severe bottleneck during domestication of rice. *Molecular Biology and Evolution* **24**: 875–888.