



Review article

Genome editing as a tool to achieve the crop ideotype and *de novo* domestication of wild relatives: Case study in tomato

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ABSTRACT

The ideotype is a theoretical model of an archetypal cultivated plant. Recent progress in genome editing is aiding the pursuit of this ideal in crop breeding. Breeding is relatively straightforward when the traits in question are monogenic in nature and show Mendelian inheritance. Conversely, traits with a diffuse, polygenic basis such as abiotic stress resistance are more difficult to harness. In recent years, many genes have been identified that are important for plant domestication and act by increasing yield, grain or fruit size or altering plant architecture. Here, we propose that (a) key monogenic traits whose physiology has been unveiled can be molecularly tailored to achieve the ideotype; and (b) wild relatives of crops harboring polygenic stress resistance genes or other traits of interest could be *de novo* domesticated by manipulating monogenic yield-related traits through state-of-the-art gene editing techniques. An overview of the genomic and physiological challenges in the world's main staple crops is provided. We focus on tomato and its wild *Solanum* (section *Lycopersicon*) relatives as a suitable model for molecular design in the pursuit of the ideotype for elite cultivars and to test *de novo* domestication of wild relatives.

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Abbreviations: CRISPR, clustered regularly interspaced short palindromic repeats; ORF, open reading frame; QTL, quantitative trait locus; SNP, single nucleotide polymorphism; TALENs, transcription activator-like effector nucleases; ZFN, zinc finger nucleases.

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1. Introduction

Genome editing is an alternative to conventional breeding in crops where a large amount of genetic/genomic resources are available. The biggest advantage of this technology is that it enables molecular breeding of crops with specific properties. Molecular breeding requires precise *a priori* knowledge of plant physiology and molecular genetics. With this knowledge and with state-of-the-art gene editing techniques, custom modifications, defined here as *molecular design*, can be targeted to specific genes to improve particular traits in a predictive manner. Molecular design differs from conventional breeding, which is empirical and where new beneficial traits are achieved through harnessing the variation resulting from traditional breeding methods, such as interspecific and intergeneric crosses or through natural, radiation and chemical mutagenesis.

The fast progress of genome editing in all fields of molecular biology was possible thanks to the development of sequence-specific nucleases, which introduce targeted double strand breaks in target loci [1]. As opposed to the older sequence-specific nucleases systems such as zinc finger nucleases (ZFNs) and meganucleases, whose specificity is difficult to engineer, TALENs and more recently CRISPR/Cas9, make it possible to target any desired sequence in the genome thanks to their easily customizable DNA binding specificities [2]. The targeted double strand breaks is repaired by non-homologous end joining of the broken DNA or by homology directed repair. The former results in short insertions or deletions (indels) causing frameshift mutations that inactivate the gene of interest, whereas the latter enables precise introduction of custom modifications. The intrinsic characteristics of TALENs, CRISPR/Cas9 and DNA repair mechanisms leading to gene editing have been described in great detail elsewhere [3,4]. Traits of commercial value have already been created using genome editing in rice [5], wheat [6], potato [7], soybean [8], and maize [9].

Here, we propose that the suite of genome editing techniques described above could be used for two purposes. Firstly, to achieve the *ideotype*, a guiding theoretical model of ideal cultivated plant, through manipulation of key monogenic traits (whose physiology has been unveiled) in elite varieties. Secondly, to manipulate monogenic domestication-related traits in wild relatives of crops harboring polygenic traits of interest. The rationale for this is that while a large number of monogenic determinants of yield have been characterized in cultivated plants, the genetic basis for valuable polygenic traits present in wild relatives (such as abiotic stress resistance) is diffuse and difficult to manipulate. Thus, instead of introducing alleles from wild relatives into cultivated crops, as has been conventionally done in classical breeding or in modern “rewilding” and “back-to-nature” crop breeding, we aim at directly manipulating wild species at the gene level to domesticate them *de novo* and harness their adaptation to adverse environments. We call this approach *de novo* domestication. Here, we present an overview of molecular design of the ideotype and *de novo* domestication for the world's top six staple crops and develop them in-depth for a genetic model species with well developed genomic resources, ease of transformation, and known target genes controlling specific traits, the tomato.

2. Molecular design in major crops and *de novo* domestication of their wild relatives

The ideotype is a theoretical model of what an ideal crop plant could be, proposed by Donald in 1968 [10]. Although originally proposed for wheat, it can be extrapolated to any domesticated crop plant. The idea behind the ideotype is that instead of selecting against defective traits, crop breeding should seek the achievement of model characters.

Cereals have been subjected to divergent selective pressure during domestication [11]. Selection in maize, sorghum and pearl millet has led to a strong increase in apical dominance, suppressing side branching and concentrating seed production on a single, large terminal head [11]. In maize, axillary branch number and length also decreased during domestication, leading to the formation of the lateral ear (which is itself an axillary branch). Wheat and rice, on the other hand, have been selected for multiple tillers (lower level branches) that distribute grain production evenly, with relatively simultaneous maturation. As will be discussed below, their height has also been reduced, as a means to avoid lodging and thus, grain losses before harvest. Perhaps the fact that the former crops have C4-type photosynthesis and the latter have C3-type is more than just a coincidence. More tillering (branching), and thus more self-shading, tends to be more detrimental to plants whose photosynthetic rate is optimized at higher irradiances, such as C4 plants. On the other hand, tillering is advantageous for weed control and to optimize the planting density. This is particularly true for crops such as paddy rice in Asia, where manual transplantation of seedling is a millenary practice which would be very inefficient for crops with a single stem. Increased agricultural mechanization for sowing and transplanting could thus lead to a concomitant alteration of the ideotype, whereby a plant with a large, thick single culm, that supports planting at higher density, would be desirable to avoid unproductive tillers, enhanced grain yield per panicle and an elevated lodging resistance [12]. This proves that the ideotype is a fluid concept which depends on the agronomic and social context.

Yield of some of the world's most important crops is restricted by abiotic stresses such as salinity and drought [13,14]. In spite of very few exceptions [15,16] resistance to such stresses tends to be of complex polygenic nature, as it involves various levels of adjustment of plant development, from the cell (e.g. Na⁺ exclusion mechanisms) to the whole plant (e.g. source-sink relationships) [17]. In most crops, the existence of wild relatives adapted to challenging environments provides suitable raw material for *de novo* domestication through molecular design (Table 1) [18]. Effective methods for delivery of DNA into a species of interest are also a prerequisite for molecular design, and plant transformation has been successfully achieved for the major crops discussed in this article [19]. A further condition is in-depth knowledge of the genetic basis of the traits to be domesticated in the crops of interest, to provide suitable targets for manipulation of their wild relatives [20]. Below we discuss these topics for the six major staple food crops: maize, wheat, rice, potato, cassava and soybean. A summary of relevant genes, the traits they control and the corresponding references is provided in the Supplementary Table S1.

2.1. The genetic basis of domestication of the three major cereal crops

Maize (*Zea mays*), wheat (*Triticum aestivum*) and rice (*Oryza sativa*) are the three most important crops in terms of worldwide grain production. Maize domestication best illustrates the kind of modifications that transform a wild plant into a cultivated one. These modifications involve changes in plant architecture, plant source-sink relationships and altered response to environmental cues. Although the morphology of the maize plant is drastically different from that of its putative wild progenitor, teosinte, classical association mapping work pinned down the differences to just six regions in the genome [21]. Subsequent studies provided a thorough characterization of some of the relevant QTLs and genes.

Among the genes that distinguish cultivated maize from its wild progenitor, two control plant architecture: *teosinte branched1* (*tb1*) and *grassy tillers1* (*gt1*). In the former, a gain-of-function mutation in a TCP-family transcription factor leads to inhibition of side branching, altering source-sink relationships and increasing yield.

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