Feature Review

Are we ready for back-to-nature crop breeding?

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Sustainable agriculture in response to increasing demands for food depends on development of high-yielding crops with high nutritional value that require minimal intervention during growth. To date, the focus has been on changing plants by introducing genes that impart new properties, which the plants and their ancestors never possessed. By contrast, we suggest another potentially beneficial and perhaps less controversial strategy that modern plant biotechnology may adopt. This approach, which broadens earlier approaches to reverse breeding, aims to furnish crops with lost properties that their ancestors once possessed in order to tolerate adverse environmental conditions. What molecular techniques are available for implementing such rewilding? Are the strategies legally, socially, economically, and ethically feasible? These are the questions addressed in this review.

Reverse breeding

Agriculture has only been practiced for about 10 000 years. In this relatively short historical period, humans have developed crops that feed more than seven billion people on this planet [1]. However, it is uncertain whether current agricultural practices will be able to feed the world in 2050, when the human population is predicted to reach more than nine billion [2–4]. Can this goal be reached without applying modern plant biotechnology techniques? Much food can be saved by reducing waste, promoting less meat-intensive diets, and using resources more efficiently; however, increased food production seems to be a necessity.

Agricultural land should not be expanded at the expense of the remaining natural ecosystems on earth. Thus, we are faced with the challenge of getting the most out of existing agricultural systems, a concept known as 'sustainable intensification' [5]. Food production is further threatened if substantial areas are used to grow crops for biofuels [6]. In contrast to industrial agricultural methods, new agricultural systems have been proposed that allow for the sustainable production of food with a minimal input of resources [7]. These include cover crops, long crop rotations, tillage, increased biodiversity, and crop and animal integration. Although the efficacy of these systems is debated, they all advocate ecosystem approaches to crop management with the aim to reduce the need for pesticides and fertilizers.

To date, the process of domestication has focused on securing specific traits that occurred at random, either spontaneously in nature or as a result of radiation treatment or exposure to mutagenic chemicals. Important traits that have been selected for are easy harvest, high yield, and low toxicity. By contrast, mutations that compromise the hereditary basis of crop survival during environmental stresses, both biotic (such as pests, pathogens, herbivores, and diseases) and abiotic (such as drought, flooding, nutrient deficiencies, and salinity) are rarely selected against. As a result, many of these survival traits may have been weakened or completely lost.

Reverse breeding as defined here implies simply back-to-nature breeding, or the reversal of the unintended results of breeding. The term 'reverse breeding' was originally introduced to describe a technique in plant cell culture where homozygous lines are produced from heterozygous parent lines [8,9]. Here, the term 'reverse breeding' includes the earlier proposed usage but goes beyond the original definition by widening the methods used to produce homozygous lines. Much remains to be learnt about

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Keywords: rewilding; reverse breeding; sustainable agriculture.

1360-1385/
http://dx.doi.org/10.1016/j.tplants.2014.11.003

the mutations in today's crop varieties that compromised or disabled valuable original traits. Detecting mutations in crop plants not found in their wild relatives will be a formidable task involving high-throughput sequencing techniques. Nevertheless, the task is becoming increasingly feasible due to rapid technological advancements and reductions in cost. Once the genes that have been mutated unintentionally have been identified, the next step would be to reestablish wild type properties. Rewilding would allow crop plants not only to better utilize available resources in the environment and have higher nutritional value, but also to better resist diseases, pests, and weeds.

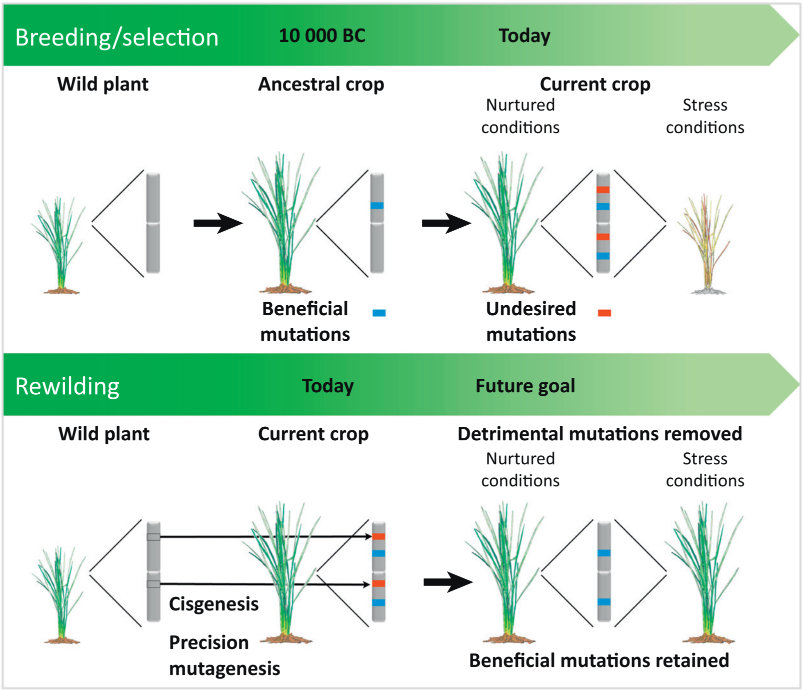
In this review, we outline an important agricultural strategy for fortifying the crops we produce today so that they can better thrive under adverse conditions. To reach this goal, we must reestablish in crop plants specific original traits that are important for plant survival under adverse conditions, while at the same time preserving other traits obtained through breeding related to food quality and yield (Figure 1). Any proposed strategy for crop modification should be evaluated based on its legal, social, economic, and ethical feasibilities (Figure 2).

The rise of agriculture and the origins of breeding

Grasses such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), rice (*Oryza sativum*), and maize (*Zea mays*) were among the first plants to be domesticated. Contrary to popular belief, domestication of grasses did not occur because of the invention of agricultural practices, but because mutant versions of grasses, with properties that made large-scale collection of grains possible, were noticed and utilized by humans.

Wheat provides an example of how the disappearance of a trait that is required for survival in the wild proved to be essential for its domestication as a crop. The first domestication of einkorn wheat (*Triticum boeoticum*), a wild relative of wheat, is believed to have taken place in southeast Turkey in around 7500 BC [10,11]. In wild wheat, the rachis (i.e., the structure to which grains are attached in the spike) becomes brittle during grain maturation, and easily shatters into spikelets that fall to the ground or blow away. Furthermore, once spikelets are collected, the grain is tightly held by the husk (glumes) surrounding it and is difficult to release. These combined features made the large-scale collection of early grains cumbersome or even impossible [1,12].

In the first domesticated einkorn wheat, *Triticum monococcum*, the rachis was hardened, and the seed was only loosely held at the base of the glumes. These properties allowed for easy harvest of wheat in the field and subsequent threshing. About 60 years ago, this trait was found to be the result of a mutation in a single gene, which was designated '*Q*' [13], and the responsible gene was identified in 2006 [14]. The *Q* gene encodes an AP2 transcription factor that regulates the expression of several other genes, which in turn influences a number of features related to inflorescence structure and flowering, including rachis fragility. Compared to the corresponding gene in wild wheat, termed '*q*', *Q* carries a dominant mutation that results in a single amino acid change in the encoded



TRENDS in Plant Science

Figure 1. Rewilding maintains beneficial mutations while eliminating undesired mutations. Ancestral crops were based on wild plants carrying mutations that proved to be beneficial for agriculture, such as mutations that made plants easier to harvest and/or resulted in higher yield. During extensive periods of breeding and inbreeding, undesired mutations accumulate and may remain unnoticed because they only affect traits that are important for the plant when growing under adverse conditions, such as nutrient and water deficiency, salinity, and the presence of pests ranging from microorganisms to herbivores. Enabling the plant to overcome these deficiencies by cisgenesis or precision mutagenesis may result in crop plants in which detrimental mutations are removed but beneficial mutations retained.