



TILLING in forage grasses for gene discovery and breeding improvement

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Mutation breeding has a long-standing history and in some major crop species, many of the most important cultivars have their origin in germplasm generated by mutation induction. For almost two decades, methods for TILLING (Targeting Induced Local Lesions IN Genomes) have been established in model plant species such as *Arabidopsis* (*Arabidopsis thaliana* L.), enabling the functional analysis of genes. Recent advances in mutation detection by second generation sequencing technology have brought its utility to major crop species. However, it has remained difficult to apply similar approaches in forage and turf grasses, mainly due to their outbreeding nature maintained by an efficient self-incompatibility system.

Starting with a description of the extent to which traditional mutagenesis methods have contributed to crop yield increase in the past, this review focuses on technological approaches to implement TILLING-based strategies for the improvement of forage grass breeding through forward and reverse genetics. We present first results from TILLING in allogamous forage grasses for traits such as stress tolerance and evaluate prospects for rapid implementation of beneficial alleles to forage grass breeding.

In conclusion, large-scale induced mutation resources, used for forward genetic screens, constitute a valuable tool to increase the genetic diversity for breeding and can be generated with relatively small investments in forage grasses. Furthermore, large libraries of sequenced mutations can be readily established, providing enhanced opportunities to discover mutations in genes controlling traits of agricultural importance and to study gene functions by reverse genetics.

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Introduction

Agronomical challenges caused by changing socio-economic and climatic environments

World food security is of increasing public concern [1]. The growing demand for food, feed and fuel, increasing scarcity of water and arable land, climate change and rising energy prices requires an increase in plant productivity, but in an ecologically sustainable way [2,3]. The development of crops with high and stable yields of good quality is a cornerstone of sustainable, intensified agricultural production. In order to realize these traits in future crops, novel tools that combine a broad range of technologies and innovative breeding strategies are needed [4].

Plant breeding – an effective tool to increase productivity

Plant breeding is the process to genetically improve crops for desired traits by selection. It mainly consists of the generation of variability in the breeding nursery, selection and extensive testing of the selected material to either be developed into a new variety or to be introduced into the next breeding cycle (Fig. 1, black). Over the past 50 years, plant breeding has attained a nearly linear increase in the yield of many major crop species such as maize (*Zea mays* L.), rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.). However, the high relative rates of yield increase during the green revolution have since been steadily declining. Moreover, yield increases are below those expected to meet the predicted demands by 2050 [5].

Grasslands are important ecosystems; worldwide, they account for 80% of milk production and 70% of meat production [6]. Perennial ryegrass (*Lolium perenne* L.) is a major component of temperate grassland systems. In forage grasses, biomass is the primary yield target, but despite intensive breeding efforts over the last decades, increases in biomass yield are below that of major crop species [7]. Due to a highly effective self-incompatibility system [8], forage grasses are mainly improved as population and synthetic varieties which is considered as one of the main reasons for the limited annual breeding progress. Moreover, self-incompatibility, by hampering self-pollination, maintains heterozygosity and recessive mutations are not directly exhibited in the phenotype.

Biotechnological opportunities to advance breeding

The rapid development of modern breeding methods, not solely based on transgenic modification, and the increasing understanding of crop genetics and genomics offer new possibilities to enhance breeding efficiency and precisely target the genes

controlling desirable traits [9]. Approaches to advance breeding can be categorized in four areas: (i) technologies to unlock and increase the genetic diversity that is available for breeding, (ii) approaches to accelerate the breeding cycle, (iii) methods to increase the selection efficiency and (iv) emerging bioinformatics tools to assist plant breeding (Fig. 1, coloured in dark red, blue, green and red, respectively). In this review, we will focus on the first area and discuss how beneficial alleles can be identified, generated and used in a breeding program. In particular, we evaluate the potential of TILLING in allogamous forage grasses, as an efficient method to induce beneficial mutations and go beyond the natural genetic diversity to advance breeding for sustainable intensification.

Exploitation of the natural genetic variation for breeding

Genetically diverse material forms the foundation of every breeding program and for centuries, breeding advances have arisen through exploitation and recombination of the natural variation available in the gene pool of a species. Natural genetic diversity is a valuable and rich source to improve traits such as environmental

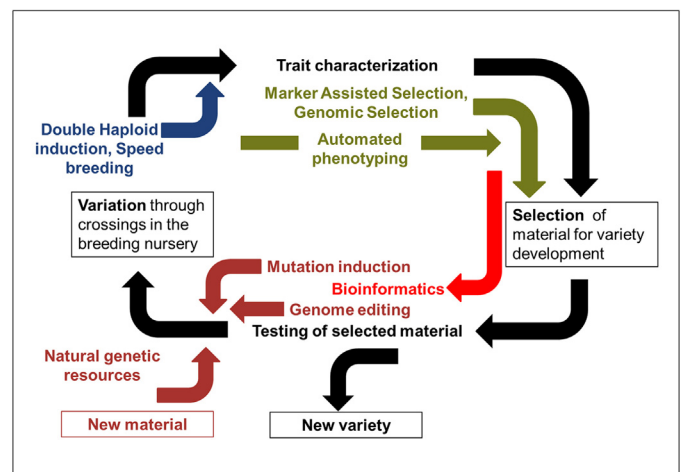


FIGURE 1

Simplified breeding cycle (black) and technological approaches (coloured) to advance plant breeding. The methods are categorized into (i) technologies to unlock and increase the genetic diversity (including exploitation of natural genetic resources, genome editing and TILLING; dark red), (ii) approaches to accelerate the breeding cycle (including speed breeding and tissue culture methods such as double haploid induction; blue), (iii) methods to increase the selection efficiency (including automated phenotyping, marker-assisted and genomic selection; green) and (iv) emerging bioinformatics tools to assist plant breeding (red).

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