



Research review paper

## Emerging technologies advancing forage and turf grass genomics

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## ABSTRACT

Grassland is of major importance for agricultural production and provides valuable ecosystem services. Its impact is likely to rise in changing socio-economic and climatic environments. High yielding forage grass species are major components of sustainable grassland production. Understanding the genome structure and function of grassland species provides opportunities to accelerate crop improvement and thus to mitigate the future challenges of increased feed and food demand, scarcity of natural resources such as water and nutrients, and high product qualities.

In this review, we will discuss a selection of technological developments that served as main drivers to generate new insights into the structure and function of nuclear genomes. Many of these technologies were originally developed in human or animal science and are now increasingly applied in plant genomics. Our main goal is to highlight the benefits of using these technologies for forage and turf grass genome research, to discuss their potentials and limitations as well as their relevance for future applications.

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### 1. Introduction

Grasslands are among the largest ecosystems on the world representing almost 40% of the terrestrial area (Reheul et al., 2010). There are three major aspects of grassland's significance; an ecological, economical and an aesthetical aspect. Grassland has a fundamental role

in soil and environment protection. It serves as an indispensable source of nutrients and water and harbors over one third of the global stock of carbon in terrestrial ecosystems (Reheul et al., 2010). Top-soil loss and water runoff is much less intensive on grassland compared to arable land (Macleod et al., 2007, 2013). Grassland is also a valuable source of biodiversity, especially in its extensive forms (Gaujour et al., 2012).

Grassland species are mainly used for forage and amenity purposes. Their rapid establishment and growth form dense swards that deliver highly nutritious, palatable and easily digestible fodder, thereby

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providing the basis for healthy meat, milk and other animal products used for human consumption. Turf grasses can be used for i) sports including golf courses and sports fields, ii) landscaping services such as lawns in parks, around homes, schools, institutions and other public areas and iii) functional purposes such as land reclamation on contaminated and derelict industrial sites and low-maintenance ground cover grown on highways and roadside shoulders, airfields and ditches. In the context of renewable energy production, biofuels and biogas obtained from biomass have gained importance to replace the petroleum-based hydrocarbons that are limited in supply and substantially contribute to undesirable carbon emissions. For biomass production, perennial grasses are advantageous due to their persistence, rapid establishment, low maintenance and harvesting efforts and their effective biomass production (Farrar et al., 2012; Searchinger et al., 2008). The aesthetical role of grassland is obvious; attractive landscapes for recreational purposes such as hiking, hunting, camping and photography as well as grazing animals on pastures are part of a multifunctional grassland agriculture that is associated with a healthy lifestyle and deeply anchored in the 21<sup>st</sup> century society. The associated ecotourism has evolved into a growing market creating new income opportunities for local inhabitants.

Most of the forage and turf grass species are cool-season grasses, native to Eurasia, and distributed in the temperate zones of both hemispheres (Reheul et al., 2010). Despite the high species richness of natural grassland, only a handful of high-yielding species constitute the main components of temporary grassland and turf production. Worldwide, the most important is perennial ryegrass (*Lolium perenne* L.) followed by its close relative Italian ryegrass (*L. multiflorum* Lam.). Agriculturally important fescues include red fescue (*Festuca rubra* L.), tall fescue (*F. arundinacea* Schreb.) and meadow fescue (*F. pratensis* Huds.). More limited in their geographic extent are Kentucky bluegrass (*Poa pratensis* L.), timothy (*Phleum pratense* L.) and orchard grass (*Dactylis glomerata* L.). Additionally, several interspecific and intergeneric hybrids appear to have a potential to compete with their parental species, including hybrid ryegrass (*L. multiflorum* × *L. perenne*) and Festulolium (*Festuca* × *Lolium*) hybrids (Thomas et al., 2003).

Many of these forage and turf grass species are characterized by an effective self-incompatibility system (Cornish et al., 1979; Lundqvist, 1961), a genetic mechanism that promotes cross pollination. Such allogamous species are usually propagated as populations and synthetic varieties, thereby maintaining high levels of heterozygosity at both the genotype and the population level. These grasses have a basic chromosome number of seven with varying ploidy levels. Both perennial and Italian ryegrass are naturally diploid, however tetraploid cultivars have been released and are widely used, especially for forage production. Ploidy levels of fescues range from diploid to dodecaploid (*F. summilusitana*). The agriculturally used species meadow fescue is diploid or autotetraploid (a few cultivars), tall fescue is hexaploid and red fescue is hexaploid or octoploid (Loureiro et al., 2007). Also other species such as orchard grass, timothy and bluegrasses display different levels of polyploidy (Huff, 2010; Huff and Bara, 1993; Kelley et al., 2009).

The genome size of grass species is generally large. Flow cytometry (FC) has been used to estimate the monoploid genome size of ryegrasses, tall and meadow fescues, ranging from  $1Cx = 2.62$  to  $3.25$  pg (Kopecný et al., 2010). The  $2C$  nuclear DNA amount of allopolyploid tall fescue ( $2n = 6x = 42$ ) was estimated to  $2C = 17.45$  pg, which is significantly less than the sum of both parental species (meadow fescue and *F. glaucescens* Boiss.). FC measurements in orchard grass vary between  $2C = 6.4$  pg and  $12.4$  pg (Horjales et al., 1995; Schifino and Winge, 1983; Tuna et al., 2004), whereas the genome size of Kentucky bluegrass depends on the ploidy level of different accessions (Murovec et al., 2009).

Similar as to other large Poaceae genomes, a vast proportion of the genome sequence might be composed of repetitive elements (International Rice Genome Sequencing Project, 2005; Ling et al., 2013; Mayer et al., 2012; Paterson et al., 2009; The International Brachypodium Initiative, 2010). These elements can be divided into tandem organized repeats and transposable elements. Tandem organized

repeats are microsatellites, minisatellites and satellites, depending on the length of the repeat unit and the number of repetitions in tandem. Transposable elements, such as retrotransposons and DNA transposons, are the most abundant repeats in plants due to their pervasiveness and constitute the main part of the genome sequence (Wicker and Keller, 2007). Schnable et al. (2009) estimated that they account for about 85% of the maize genome. First insights into the repetitive content of forage and turf grass genomes came from shotgun sequencing efforts on chromosome 4F of meadow fescue, identifying the Ty3/Gypsy-like elements as the major type of repeats (Kopecný et al., 2013). However, only a complete genome sequence will allow for a detailed description of the size and complexity of forage and turf grass genomes.

Due to the highly heterozygous, large and complex nature of forage and turf grass genomes, genome research is complicated and the genomic resources available for these species are lagging far behind those of model species and major crops such as rice (*Oryza sativa* L.), maize (*Zea mays* L.), wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.). However, recent technological and methodical developments have initiated a novel era of genomic research in “orphan” grass species. Therefore, this review aims at i) identifying key technologies and methods that have significantly progressed our understanding of crop genomics ii) evaluating prospects for practical applications of these technologies in forage and turf grasses and iii) discussing future directions of forage and turf grass genomics. This review will not attempt to provide a fully comprehensive list of current technologies, but will aim to describe the key benefits and features of carefully selected technologies applied to advance forage and turf grass genomics.

## 2. Emerging technologies advancing forage and turf grass genomics

### 2.1. Flow cytometry

Flow cytometry (FC) has become a ground-breaking technology for genome analyses of large and complex grass genomes (Dolezel et al., 2012). It provides opportunities to reduce the complexity by dissecting the genome into individual chromosomes. FC enables the purification of a large number of copies of desired chromosomes by flow sorting. To be successful, individual chromosomes have to be accurately resolved from one another in a karyotype. This is difficult in plant species where chromosomes are often similar in size and relative DNA content. For example, only one out of the 21 chromosomes of wheat can be discriminated (Vrana et al., 2000) and one out of seven chromosomes can be resolved in ryegrass and meadow fescue (Kopecný et al., 2013). This limitation can be overcome by sorting chromosomes from altered karyotypes where target chromosomes differ from the rest of the set, or by improvement of the instrumentation and methodology (Dolezel et al., 2012). Recent progress in flow sorting of chromosomes has been stimulated mainly by the use of cytogenetic stocks including deletions, translocations, alien chromosome and chromosome arm additions. The dissection of crop genomes into individual chromosomes was enabled by using those stocks in barley, wheat, rye, maize and pea (Kubalaková et al., 2002, 2003; Li et al., 2001; Neumann et al., 1998; Suchanková et al., 2006). However, the plasticity of grass genomes, including a certain tolerance of aneuploidy and a rather relaxed chromosome pairing system, limit the development of such cytogenetic stocks in forage and turf grasses. Thus, the only option to resolve individual chromosomes from one another in grasses is to use alternative approaches. The most promising is the application of fluorescent *in situ* hybridization in suspension (FISHIS) and sorting of chromosomes based on the fluorescent signal of various DNA probes (Giorgi et al., 2013; Ma et al., 2005). Protocols to dissect meadow fescue and perennial ryegrass genomes using labeled tandem repeats and microsatellites are currently being developed (Kopecný et al., unpublished). Much success was already met in durum wheat (*Triticum turgidum* L. var. *durum*), where all 14 chromosomes can be sorted using GAA microsatellites. This is a breakthrough for all species with large and complex genomes

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