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REVIEW ARTICLE

Molecular mechanisms of biomass increase in plants

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Abstract Biomass consumption continues to increase worldwide for the provision of human energy needs. These high pressures for energy will determine the demand for crop plants as a resource for biofuel, heat and electricity. Thus, the search for plant traits associated with genetic increases in yield is unconditional. Here, we propose exploiting recent advances in plant biomass enhancement in non-crop as well as in crop plants. For this purpose, biotechnological approaches that are well known rapid ways of enhancing the plant traits, as well as the traditional way of improving plants through plant breeding selecting for desirable phenotypes are excellent techniques to improve plant biomass and reduce the dependence on fossil fuels. Obviously, many genes can be associated with promising phenotypes however this review will focus on genes selected from different plant networks.

Introduction

25 Renewable energy can be produced from a wide variety
26 of sources including wind, solar, hydro, tidal, geother-
27 mal and biomass (Kammen & Sunter, 2016). The biomass
28 is derived from waste and residues of biological origin

(e.g. agricultural residues, forest biomass, energy crops, 29
algae cultivated in bioreactors, animal matter), but for this 30
article we will restrict the term biomass to the vegetable 31
matter used as source of energy. Currently, energy crops 32
are used on a large scale for electricity or heat production 33
and to biofuel conversion (Kocar & Civas, 2013). Enhance- 34
ment of agriculture practices and improvement of cultivars 35
are crucial for a genuine large expansion of biomass sup- 36
ply. Actually, increased biomass production is dependent of 37
improvements and agricultural practices and genetic mod- 38
ifications that would increase plant growth and produce 39
augmented plant dry matter. Plant growth can be defined 40

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as an irreversible increase in the size of the plant, involving cell division and increase in cell sizes.

In the last few decades, plant breeders have been able to introduce desirable traits into plants through genetic modification using a variety of techniques commonly known as plant biotechnology. These techniques have emerged as practical tools to boost plant yields and currently can be used to increase plant biomass and to alter plant cell wall features, in order to increase the efficiency of biofuel production (Allwright & Taylors, 2016; Furtado et al., 2014; McKendry, 2002).

An example of success is the use of biomass for electricity and or biofuel production in Brazil, as part of a strategic program to reduce dependence on fossil fuels. The total installed power in Brazil in 2015 was 140.9 GW from which 13.3 GW corresponds to biomass (9.4%) (MME, 2015). Among the biomass sources, 80% is derived from sugarcane bagasse, which was able to provide 13.7 TWh for sugar industries and 20.4 TWh for the national electrical system (UNICA, 2015). The total ethyl alcohol production from sugarcane within this period reached 30.3 million cubic meters, from which 11.6 and 18.7 million cubic meters corresponds to hydrated alcohol and anhydrous alcohol respectively (MME, 2015).

The choice for plant biomass is a basic ingredient for sustainable development and it will enable the diversification of the energy matrix. For this reason, governments and private research centers recognize the potential of this source and support many projects in plant biotechnology (IEA, 2016; MCTI, 2016; US Biomass Program 2016). As a result of these investments, several approaches were adopted to increase biomass through plant genetic engineering and genome edition (Ishida, Hiei, & Komari, 2007; Liu, Hu, Palla, Tuskan, & Yang, 2016; Mayavan et al., 2015; Zhu et al., 2016). These can include the genetic modification of photosynthetic pathways, cell architecture or plant growth regulators. However, these approaches involve changing complex traits, usually in production environments that are highly variable and unpredictable. A very large number of genes are involved in the control of plant growth and productivity in agriculture and the aim of this review is to give an overview of the most promising genes or traditional ways (Table 1).

Cell cycle genes

The cell cycle is conserved in all eukaryotes and the basic components are DNA synthesis phase (S) and mitosis (M), separated by postmitotic interphase (G1) and premitotic interphase (G2) gap phases (Scofield, Jones, & Murray, 2014). To ensure that the phases are carried out to completion with accuracy and in the proper order, its transition is feedback regulated at checkpoints (Doerner, 1994; Sablowski & Dornelas, 2014). The major transitions are G2/M, when proliferative cells achieve mitotic competence, and G1/S, when cells gear up for nuclear DNA replication (Francis, 2007; Gutierrez, 2016). Many of the molecular players and mechanisms are also conserved, particularly the CYCLIN-DEPENDENT KINASES (CDKs) and its noncatalytic partner, CYCLINS (CYCs), and the multi-subunit E3 ubiquitin ligase ANAPHASE-PROMOTING COMPLEX/CYCLOSOME (APC/C) (Inagaki & Umeda, 2011; Inze & De Veylder, 2006; Lima et al., 2010). The cell cycle is directly responsible

for the number of cells, which together with cell expansion determines overall organ size and growth rate. Therefore, the regulation of cell cycle is fundamental to understand the plant growth and the impact on yield components. In plants, one of the major regulators of CDK activity are INHIBITOR OF CDK/KIP-RELATED PROTEIN (ICK/KRP) molecules that bind and inhibit or sequester CDKs (Verkest, Weinel, Inze, De Veylder, & Schnittger, 2005). Down-regulation of multiple ICK genes *ick1/ick2/ick6/ick7* and *ick1/ick2/ick5/ick6/ick7* in Arabidopsis increased CDK activity, stimulated cell proliferation and resulted in larger organs and seeds (Cheng et al., 2013). The entry into the S phase is controlled by E2F transcription factors that act as positive regulator of cell proliferation (Vandepoele et al., 2005). The ectopic expression of Arabidopsis *E2FB* gene in tomato accelerated plant development, leading to higher fruit yield, producing bigger and heavier fruits than in control plants (Abraham & del Pozo, 2012).

The APC/C is an E3 ubiquitin ligase that control de cell cycle transitions by targeting specific substrates for degradation by the 26S proteasome (Eloy, Lima, Ferreira, & Inze, 2015). Overall, the APC/C subunits have been conserved in the course of evolution, although gene duplication of different subunits has occurred in some plants (Lima et al., 2010). When the Arabidopsis *APC3a/CDC27a* gene is overexpressed in tobacco it accelerated plant growth, leading to plants with increased biomass production (Rojas et al., 2009). Similar results were obtained when tobacco plants overexpressing the *APC10* gene from Arabidopsis increased biomass and reduced life cycle length (Lima, Eloy, Bottino, Hemerly, & Ferreira, 2013). Interesting, co-overexpression of *APC10* and *APC3a/CDC27a* genes in tobacco resulted in an increased number of fruits and shoot length (Lima et al., 2013). In Arabidopsis, the overexpression of *APC10* enhanced the leaf size and the rates of cell division (Eloy et al., 2011). SAMBA was described as a negative regulator of the APC/C in Arabidopsis and mutant plants produced larger seeds, leaves and roots (Eloy et al., 2012). In addition, *DA1* encodes a ubiquitin receptor that restricts cell proliferation and *EOD1/BIG BROTHER (BB)* encodes an E3 ligase that limits organ size (Disch et al., 2006; Li, Zheng, Corke, Smith, & Bevan, 2008; Vanhaeren et al., 2016b). Gene stacking for the triple gene mutant combination of *SAMBA*, *DA1* and *BB* showed bigger plants and accumulated more biomass in root system compared to control (Vanhaeren et al., 2014; Vanhaeren, Inze, & Gonzalez, 2016a; Vanhaeren et al., 2016b). This result reveals that in absence of one APC/C inhibitor (*samba*) and two cell cycle regulators (*da1-1* and *eod1-2*), mutant plants altered their organs size and the biomass increased significantly (Vanhaeren et al., 2016a).

Hormone

Plant growth and development involves the integration of endogenous and environmental signals, and genetic set (Gray, 2004). Fundamental to this integration are several growth regulators called plant hormones including abscisic acid (ABA), ethylene, gibberellins (GAs), auxin (IAA), cytokinins, and brassinosteroids (BRs) that can exert strong, seemingly independent actions on physiological and biochemical processes in the plant (Vanstraelen & Benkova, 2012). Although there are hormones that increase

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