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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

Renewable energy can be produced from a wide variety of sources including wind, solar, hydro, tidal, geothermal and biomass (Kammen & Sunter, 2016). The biomass is derived from waste and residues of biological origin (e.g. agricultural residues, forest biomass, energy crops, algae cultivated in bioreactors, animal matter), but for this article we will restrict the term biomass to the vegetable matter used as source of energy. Currently, energy crops are used on a large scale for electricity or heat production and to biofuel conversion (Kocar & Civas, 2013). Enhancement of agriculture practices and improvement of cultivars are crucial for a genuine large expansion of biomass supply. Actually, increased biomass production is dependent of improvements and agricultural practices and genetic modifications that would increase plant growth and produce augmented plant dry matter. Plant growth can be defined

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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 be 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, Weinl, 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

Table 1 List of promising candidates for plant growth promotion.

Plant species	Gene modification	Phenotype	Reference
Cell cycle genes			
Arabidopsis	*ick1/ick2/ick6/ick7* mutant	ICK genes can modulate the mitotic cycle as well as endocycle in plants. Knockout more than three ICK is sufficient to enhance the growth of seedlings.	Cheng et al. (2013)
	ick1/ick2/ick5/ick6/ick7 mutant		
Arabidopsis	*bb* mutant	BIG BROTHER (BB) is E3 ubiquitin-ligase and repressor of plant organ growth. Homozygous mutants showed larger petals and sepals than wildtype.	Disch et al. (2006)
Arabidopsis	*da1* mutant	DA1 is a ubiquitin receptor which sets final seed and organ size by restricting the period of cell proliferation. Mutant plants increased seed and organ size.	Li et al. (2008)
Arabidopsis	*samba* mutant	SAMBA is a plant-specific negative regulator of APC/C. Samba mutants produced larger seeds, leaves, and roots.	Eloy et al. (2012)
Arabidopsis	*APC10*OE	APC10 subunit enhanced rates of cell division and increased leaf size.	Eloy et al. (2011)
Tobacco	Overexpression of *APC3a/CDC27a* gene from Arabidopsis	Plants overexpressing *CDC27a* subunit exhibited increased growth rates and increased organ size.	Rojas et al. (2009)
Tobacco	Overexpression of *APC10* gene from Arabidopsis	Transgenic plants had an accelerated growth rate and had higher fresh and dry total mass accumulation as compared to the control.	Lima et al. (2013)
Tomato	Overexpression of *E2FB* gene from Arabidopsis	The *E2FB* regulates cell division and cell differentiation. The E2FB-overexpressing plants accelerated tomato plant development.	Abraham and del Pozo (2012)
Hormone			
Arabidopsis and poplar	Overexpression of *GA 20-OXIDASE* gene from pine	Transgenic Arabidopsis and poplar plants expressing GA 20-oxidase resulted in a large increase of biomass.	Jeon et al. (2016)
Arabidopsis and tobacco	Overexpression of *DWF4* gene from Arabidopsis	C-22 hydroxylation of BRs is catalyzed by DWF4. Ectopic overexpression of DWF4 resulted in an increase in seed yield and more biomass.	Choe et al. (2001)
Poplar	Overexpression of *GA 20-OXIDASE* gene from Arabidopsis	Overexpression of a *GA 20-OXIDASE*, a key enzyme in GA biosynthesis, resulted in trees with faster growth in height and diameter, larger leaves, more numerous and longer xylem fibers, and increased biomass.	Eriksson et al. (2000)
Maize	Overexpression of *GA 20-OXIDASE* gene from Arabidopsis	Plants accumulated more vegetative biomass, cellulose and lignin than control.	Voorend et al. (2016)
Rapeseed	Overexpression of *DWF4* gene from Arabidopsis	Plants displayed increased seed yield, higher root biomass and root length	Sahni et al. (2016)
Switchgrass	Overexpression of *GA 20-OXIDASE* gene from maize	Transgenic plants exhibited longer leaves, internodes, which resulted in more biomass.	Do et al. (2016)
Tobacco	RNAi silencing of *GA 2-OXIDASE* gene	Knockdown of *GA 2-OXIDASE* substantially increased tobacco growth and fiber production.	Dayan et al. (2010)
Regulation of transcription			
Arabidopsis	Overexpression of *AP2L1* gene from larch	Overexpression of *AP2L1* is sufficient to increase the size of aerial organs by enhancing organ growth and development.	Li et al. (2013)
Arabidopsis	Overexpression of *WRKY76* gene from sunflower	Transgenic plants expressing *WRKY76* exhibit increased biomass and seed yield	Raineri et al. (2015)
Arabidopsis	Overexpression of *HB11* gene from sunflower	Transgenic plants showed tolerance to flooding stress and exhibited higher biomass compared to control.	Cabello et al. (2016)
Arabidopsis and poplar	RNAi silencing of *SHR* gene	Down-regulation of *SHR* lead to a coordinated acceleration of plant growth and increased fresh biomass	Wang et al. (2011)

Table 1 (*Continued*)

Plant species	Gene modification	Phenotype	Reference
Poplar	*BEE3L*OE	Overexpression of *BEE3L* promoted vegetative growth and enhanced xylem cells in stem.	Noh et al. (2015)
Tobacco	Overexpression of *NAC* gene from *Lepidium latifolium*	Plants accumulated more biomass and are more tolerant to abiotic stresses compared to wild type.	Grover et al. (2014)
Tobacco	Overexpression of *bHLH57* gene from finger millet	Transgenic plants were tolerant to high salinity and accumulated more biomass under stress condition.	Babitha et al. (2015)
Wheat	*NAC69-1*OE	Overexpression resulted in the enhanced length of roots, more aboveground biomass and grains.	Chen et al. (2016)
Photosynthesis			
Arabidopsis	*tap38* mutant	Increment in thylakoid electron flow improving photosynthetic performance and growth under low light conditions.	Pribil, Pesaresi, Hertle, Barbato, and Leister (2010)
Arabidopsis	*35S:AtFKBP16-1* overexpression	Higher acclimation under photosynthetic stress conditions.	Seok et al. (2014)
Arabidopsis	From to five chloroplast-targeted bacterial genes introduction, glycolate catabolic pathway was introduced into Arabidopsis chloroplasts.	Occurred reduction, but not eliminated metabolic photorespiratory flux reducing carbon loss. Transgenic plants showed enhanced of CO_2 assimilation resulting in faster growth correlated to more shoot and root biomass.	Kebeish et al. (2007)
Arabidopsis	In mutants with Rubisco activase absence, thermostable variants of this enzyme were introduced in deletion line.	Rubisco activase thermostability improved photosynthetic rates and increased plant biomass and seed yield.	Kurek et al. (2007)
Maize	Overexpressed a rice trehalose-6-phosphate phosphatase in maize ears using a floral promoter.	High sucrose levels in ear spikelets resulting in the increased kernel set and harvest index.	Nuccio et al. (2015)
Potato	Glycolate dehydrogenase complex was complemented into mutants to different genes of this complex. An engineered polyprotein retained the complex function in plant plastids.	Improving CO_2 uptake and higher photosynthesis related metabolites levels. It resulted in the more shoot, leaf and tuber biomass.	Nolke, Houdelet, Kreuzaler, Peterhansel, and Schillberg (2014)
Rice	Manipulation of amount of Rieske FeS protein in the cytochrome *b6/f* complex	CO_2 assimilation strongly coupled with plant growth and grain yield.	Yamori et al. (2016)
Rice	*HYR*OE	Transgenic plants showed higher grain yield, enhanced drought-resistant and improved biomass.	Ambavaram et al. (2014)
Tobacco	Expression of *VDE*, *ZEP*, and *PsbS* genes from Arabidopsis	Transgenic lines showed increases in leaf area and plant height relative to control.	Kromdijk et al. (2016)
Metabolism			
Arabidopsis	Overexpression of *SBEI* or *SBEIIb* genes from maize in Arabidopsis mutants *sbe2.1/sbe2.2*	Plants overexpressing maize starch branching enzymes showed enhanced biomass and oilseed production.	Liu et al. (2015)
Arabidopsis and tobacco	Overexpression of *NLP7* gene from Arabidopsis	Overexpression of NLP7 enhances N assimilation and growth of transgenic Arabidopsis and tobacco plants.	Yu et al. (2016)
Arabidopsis and poplar	Overexpression of *SPS* and *SPP* genes from Arabidopsis	The fusion construct between *SPS* and *SPP* genes promotes plant growth in both transgenic Arabidopsis and hybrid poplar.	Maloney et al. (2015)
Cotton	*SUSA1*OE	Overexpression of *SUSA1* leads to increased cotton biomass yield	Jiang et al. (2012)

Table 1 (*Continued*)

Plant species	Gene modification	Phenotype	Reference
Maize	*Gln1-3OE*	A significant increase in grain yield was observed when compared to wild-type.	Martin et al. (2006)
Poplar	Overexpression of *GS* gene from pine	Poplars expressing cytosolic pine *GS* showed higher vegetative growth than control plants in a field trial.	Jing et al. (2004)
Potato	Two triple-transgenic lines overexpressing pea *GPT* and Arabidopsis *NTT1* genes, and *EcPPase* or *aStAGPase*	Transgenic potato plants increased the tuber yield and starch content.	Jonik et al. (2012)
Sorghum		The overexpression of *GS* resulted in improved growth and biomass accumulation.	Urriola and Rathore (2015)
Switchgrass	*SUS1*OE	Transgenic switchgrass plants increased biomass and cellulose content.	Poovaiah et al. (2015)
miRNA			
Alfafa	miRNA156OE	Transgenic alfalfa plants had increased root length and elevated biomass production	Aung et al. (2015)
Arabidopsis	miRNA156OE	miRNA156 overexpression caused a moderate delay in flowering and more dry biomass	Schwab et al. (2005)
Arabidopsis	miRNA397bOE	Transgenic plants reduced lignin deposition and improved grain yield and biomass	Wang et al. (2014)
Arabidopsis	miRNA858aOE	Transgenic plants overexpressing miR858a showed an elevated vegetative growth phenotype	Sharma et al. (2016)
Poplar	miRNA156OE	Transgenic plants had shorter internode length and reduction in stem lignin content	Rubinelli et al. (2013)
Red clover	miRNA156OE	Overexpression significantly delayed flowering, improve nutritive quality, and increase forage biomass production.	Zheng et al. (2016)
Rice	miRNA397OE	Overexpression enlarged grain size and promoted panicle branching	Zhang et al. (2013)
Switchgrass	miRNA156OE	The plants had a drastic increase in tiller numbers and more biomass	Fu et al. (2012)

productivity, only a few were linked to the increase of aerial biomass such as GAs and BRs. The GAs function as plant hormones playing important roles in regulation of seed germination, leaf expansion, stem elongation, flower and fruit development, and wood formation (Hedden & Sponsel, 2015). Therefore, it is important for plants to produce and maintain optimal levels of bioactive GAs to ensure normal growth and development. One potential control point in the regulation of GAs biosynthesis is the rate limiting enzyme GIBBERELLIN 20-OXIDASE (GA 20-OXIDASE), which catalyzes the formation of bioactive GAs. Hybrid poplar plants overexpressing *GA 20-OXIDASE* from pine or Arabidopsis increased the total biomass although leaf area was significantly decreased (Eriksson, Israelsson, Olsson, & Moritz, 2000; Jeon et al., 2016). Similar results were found in transgenic maize and switchgrass lines overexpressing the Arabidopsis and maize *GA 20-OXIDASE*, respectively. However, regrettably, these transgenic maize plants had taller and more slender stems (Do, De Tar, Lee, Folta, & Zhang, 2016; Voorend et al., 2016). Another approach to keep high levels of bioactive GAs is the reduction of GIBBERELLIN 2-OXIDASE expression (GA 2-OXIDASE), which acts inactivating endogenous bioactive GAs (Schomburg, Bizzell, Lee, Zeevaart, & Amasino, 2003). Aiming at this, Dayan, Schwarzkopf, Avni, and Aloni (2010) generated tobacco RNAi lines for Arabidopsis *GA 2-OXIDASE* and crossed them with lines overexpressing Arabidopsis *GA 20-OXIDASE* in order to study the benefits of silencing GA 2-OXIDASE. The resulting plants with increased biomass than control plants, although the silencing GA 2-OXIDASE expression promoted faster growth as compared with the overexpression of GA 20-OXIDASE and a slight additive effect when co-overexpressed with GA 20-OXIDASE (Dayan et al., 2010).

The BRs are a group of plant steroid hormones that regulate stem and root growth, floral initiation, and the development of flowers and fruits (Zhu, Sae-Seaw, & Wang, 2013). It is known that BRs bind to the BRASSINOSTEROID-INSENSITIVE 1 (BRI1) receptor kinase, which functions in combination with the co-receptor BRASSINOSTEROID-ASSOCIATED KINASE1 (BAK1) in hormone perception and signal transduction (Li et al., 2002). In rice, the *d61-7* (*bri1*) mutants increased light capture for photosynthesis by developing erect leaves, producing 35% higher biomass than control plants at high planting density (Morinaka et al., 2006). Another important player is DWARF4, which encodes an enzyme that catalyzes a rate-limiting step in BR biosynthesis. The effect of Arabidopsis *DWF4* overexpression in Arabidopsis, tobacco, rice and rapeseed showed, at the termination of flowering, larger leaves, high number of branches and grain yield than control (Choe et al., 2001; Sahni et al., 2016; Sakamoto et al., 2006).

Regulation of transcription

Transcription is the initial step in which genes are selected for expression and for modulation of levels of expression (Joshi et al., 2016). Thus, it is crucial to understand which transcription factors (TFs) might be involved in biomass accumulation.

One interesting class of transcription factors is APETALA2/ETHYLENE-RESPONSIVE ELEMENT BINDING PROTEIN (AP2/EREBP), which plays crucial roles in plant growth, development and response to such diverse stresses such as extreme temperature, drought, high salinity and pathogen infection (Dietz, Vogel, & Viehhauser, 2010; Licausi, Ohme-Takagi, & Perata, 2013). Overexpression of the larch AP2/EREBP transcription factor *AP2L1* in Arabidopsis led to markedly enlarged organs, increased biomass, and improved seed production greater than 200% (Li et al., 2013).

Manipulation of WRKY TFs levels, which regulates both biotic as well as abiotic responses through an intricate gene network, is promising as well (Phukan, Jeena, & Shukla, 2016). Transgenic lines expressing the sunflower WRKY transcription factor member *WRKY76* in Arabidopsis exhibited increased biomass and seed yield (Raineri, Ribichich, & Chan, 2015). In rice, plants overexpressing *WRKY74* grew better in lower phosphorus concentration and accumulated more biomass than control plants (Dai, Wang, & Zhang, 2016). These results indicate WRKY TFs as potential biotechnological tools to improve tolerance of crops to abiotic stresses and increase the biomass. NAM-ATAF1/2-CUC2 (NAC) family genes control morphological and anatomical changes, especially growth of the secondary cell walls (Singh, Grover, & Nasim, 2016). In wheat, expression of the rice ROOT-SPECIFIC UNKNOWN PROTEIN 3 (RSP3) gene driven by the promoter of *NAC69-1* produced 32% and 35% more aboveground biomass and grains, respectively (Chen et al., 2016). In addition, tobacco plants overexpressing a NAC gene isolated from *Lepidium latifolium* had longer leaves and added fresh weight during vegetative phase (Grover et al., 2014).

The family of the BASIC HELIX-LOOP-HELIX (bHLH) TFs regulates distinct cellular processes such as cell wall biosynthesis, responses to abiotic and biotic stress and hormone signaling (Pireyre & Burow, 2015). Overexpression of bHLH transcription factor *BRASSINOSTEROID ENHANCED EXPRESSION 3* (*BEE3L*) exhibited a significant increase of total dry weight of stems (1.24–1.45 fold higher) and roots (1.22–1.86 fold higher) compared to wild-type poplar plants (Noh, Choi, Cho, & Lee, 2015). Plants overexpressing a *bHLH57* gene from finger millet in tobacco increased the tolerance to salinity and showed higher photosynthetic activity, leading to increased biomass (Babitha, Vemanna, Nataraja, & Udayakumar, 2015). Among the extensive list of TFs families, HOMEODOMAIN-LEUCINE ZIPPER (HD-Zip) and GAI-RGA-SCR (GRAS) are important in cellular processes and cause morph physiological alterations in plants (Brandt, Cabedo, Xie, & Wenkel, 2014; Hirsch & Oldroyd, 2009). Arabidopsis transgenic lines overexpressing sunflower HD-Zip member *HB11* increased rosette and stem biomass, and showed tolerance to flooding (Cabello, Giacomelli, Piattoni, Iglesias, & Chan, 2016; Henriksson et al., 2005). In addition, when the GRAS family member *SHORT-ROOT* (*SHR*) gene was silenced in poplar trees the strongest RNAi line accumulated almost 60% more above ground fresh biomass (Wang et al., 2011).

Photosynthesis

Plant carbon assimilation occurs mainly by photosynthesis and energy demand for growth is supported by photosynthetic metabolism. Photosynthesis is divided in two steps, the first phase comprises light uptake and electron transport around photosystems, the second phase is related to CO_2 assimilation in Calvin–Benson Cycle.

Light uptake into the photosystems is promoted by chlorophyll and carotenoids associated in the harvesting complexes in the thylakoid membranes. In this process, water splitting occurs in photosystem II to derivate electrons that will be conduct by linear electron flow to photosystem I, resulting in NADPH and ATP production (Yamori & Shikanai, 2016). Structural components of light reactions centers are highly conserved among plant species (El-Lithy et al., 2005; Leister, 2012; Rosado-Souza et al., 2015). Fujimoto, Taylor, Shirasawa, Peacock, and Dennis (2012) suggested that the increase of biomass in *Arabidopsis thaliana* hybrids, compare to parental lineages, is not related with photosynthetic rates per unit leaf area. The increase in cell size was attributed to an increase in the number of chloroplasts per cell and to higher total chlorophyll levels (Fujimoto et al., 2012). During growth, plant leaves can be shaded by clouds or other leaves and the protective dissipation is maintained by some minutes reducing photosynthesis. Recently, it was showed that a more rapid reduction in protective dissipation on transfer of leaves from high light to shade lead tobacco plants to a faster recovery of photosynthetic efficiency and to improvement of 15% in productivity (Kromdijk et al., 2016). By relatively low natural variability in photosystems components, it was suggested an indirect role to conventional breeding on the improvement of the light-dependent reactions efficiency around photosystems (Leister, 2012). In contrast, it was indicated the direct involvement of genetic engineering to enhancing crop biomass accumulation mediated by photosynthesis light reactions improvement (Driever, Lawson, Andralojc, Raines, & Parry, 2014; Leister, 2012).

In wheat, most of the variation in photosynthetic rates found among 64 elite cultivars was explained by components related to maximum capacity and operational rates of CO_2 assimilation (Driever et al., 2014).

The capacity of CO_2 assimilation is limited primarily by a relative slower Rubisco carboxylation rate and natural variation on kinetic properties of Rubisco had been little explored by plant breeders (Jez, Lee, & Sherp, 2016; Nunes-Nesi et al., 2016; Ort et al., 2015). A recent study characterized Rubisco catalytic properties of 75 plant species represented by crop and undomesticated plants. Crop plant enzymes exhibited lower Rubisco catalytic properties compared to non-crop plants suggesting the potential of these enzymes to ameliorate crop photosynthesis efficiency (Orr et al., 2016). From the cyanobacterium *Synechococcus elongatus* PCC7942, a faster Rubisco replaced the tobacco Rubisco natural enzyme and led the plants to higher rates of CO_2 fixation (Lin, Occhialini, Andralojc, Parry, & Hanson, 2014). In rice, the CO_2 assimilation revealed a strong correlation with

transcription factor HIGHER YIELD RICE (HYR) and the high expression of this gene enabled the enhancing photosynthesis capacity and biomass accumulation of the plant different organs, such as root, shoot and grains (Ambavaram et al., 2014). In this context, many strategies to improve CO_2 assimilation parallel to plant biomass increment have failed due to the limited capacity of some species in utilizing photosynthesis products (Kirschbaum, 2011). Therefore, the increase in photosynthetic rates must be followed by a high capacity of carbon utilization, which apparently is correlated to plants with more growth capacity. Thus far, strategies aimed at increasing biomass through the improvement of photosynthetic rates been scarcely explored by conventional breeding and exploitation of natural variation. In Table 1, some advances in genetic engineering to improve plant photosynthesis parallel to biomass increase are summarized. Together, conventional breeding and molecular genetics can useful to understand plant photosynthesis peculiarities and to resort to resolved the major photosynthetic deficiencies allowing the development of crops plant with higher biomass gain levels.

Metabolism

Plants retain a sophisticated and complex network of chemical reactions that provide energy for vital processes and for synthesizing new organic material. Two essential nutrients, Carbon (C) and nitrogen (N), are essential for plant survival and C/N balance is also critical for plant growth (Zheng, 2009). For plants, the partitioning of carbon fixed in photosynthesis and the maintenance of respiration costs of plant cells will have a significant influence on the rate of plant biomass accumulation. Following this logic, starch can be seen as an overflow product synthetized when the rate of CO_2 fixation exceeds the rate of sucrose synthesis and the regulation of key enzymes present in these biosynthetic pathways is critical (Stitt, 2013). On the other hand, nitrogen availability is a strong determinant of plant biomass partitioning and may depend on a direct incorporation of absorbed N or amino acid into roots. Thus, the source-to-sink nitrogen partitioning is essential for plant growth and development and directly influences grain production (Distelfeld, Avni, & Fischer, 2014).

The NIN-LIKE PROTEIN 7 (NLP7) modulates nitrate sensing and metabolism, and acts as an orchestrator of nitrate responses (Yu et al., 2016). Overexpression of Arabidopsis *NLP7* gene enhances N assimilation and growth of transgenic tobacco and Arabidopsis plants (Yu et al., 2016). Other key enzyme in nitrogen metabolism is the GLUTAMINE SYNTHETASE (GS). Analysis of tobacco transgenic lines overexpressing the pea cytosolic *GS1* gene showed the highest increases in plant fresh weight, and dry weight under nitrogen-limiting and nitrogen-non-limiting conditions compared with control (Oliveira, Brears, Knight, Clark, & Coruzzi, 2002). In addition, tobacco plants overexpressing alfalfa *GS* gene under nitrogen starvation had 70% higher shoot content and 50% more leaf area (Urriola & Rathore, 2015). In addition, transgenic poplars expressing a pine *GS* gene reached average heights 21–41% greater than control and maize plants overexpressing *Gln1-3* gene in leaves increased kernel number by 30% (Jing et al., 2004; Martin et al., 2006).

Soluble sugars and starch play a central role in carbon metabolism regulating cellular physiology. Starch is the main form by which plants store carbohydrate and is a major photosynthetic product in many plant species. During the day, plants store part of the photo assimilates in starch and degrade it to supply sugars for growth at night. Interesting, the starch degradation is under circadian control and starch content is negatively correlated with biomass (Graf, Schlereth, Stitt, & Smith, 2010; Sulpice et al., 2009). Thus, in addition to its function on carbon and energy storage, starch may also important for plant growth and productivity. When endogenous isoforms of Arabidopsis STARCH BRANCHING ENZYME (SBE) were substituted by either one of maize endosperm-enzymes SBEI or SBEIIb the shoot dry weights of transgenic plants are significantly higher than in wild-type plants, around 80% and 150% (Liu et al., 2015). Arabidopsis and hybrid poplar plants overexpressing a *SUCROSE PHOSPHATE SYNTHASE* (*SPS*) and *SUCROSE PHOSPHATE PHOSPHATASE* (*SPP*) increased plant growth and biomass accumulation (Maloney, Park, Unda, & Mansfield, 2015). In cotton, plants overexpressing *SUCROSE SYNTHASE* (*SUS*) *A1* showed increased biomass during the seedling and boll stages (Jiang, Guo, Zhu, Ruan, & Zhang, 2012). Also, transgenic switchgrass plants overexpressing *SUS 1* increased plant height by up to 37% and biomass up to 13.6% (Poovaiah et al., 2015). Plant productivity is dependent on source-sink relationships and the manipulation of target genes involved in sugar transport and metabolism affects directly plant growth (Flugge, Hausler, Ludewig, & Gierth, 2011; Jonik, Sonnewald, Hajirezaei, Flugge, & Ludewig, 2012; Yu, Lo, & Ho, 2015). This finding is consistent with the work of Jonik et al. (2012), who described that increasing the source and sink capacities the doubling in tuber starch yield was achieved.

Hybridity and ploidy

Many of our current agricultural crops are natural or agricultural hybrids, or polyploids. In plants, hybridization is often considered a complex and multigene trait, involving changes in numerous quantitative traits, such as vegetative growth rate, biomass, seed size, and tolerance to stresses (Baranwal, Mikkilineni, Zehr, Tyagi, & Kapoor, 2012). In the other hand, polyploidy refers to the presence of more than two complete sets of chromosomes per cell nucleus (Soltis et al., 2009). Both hybridity and ploidy affect cell number, size, and growth vigor in plants, and the consequence can be a superior performance in biomass accumulation.

To test the effects of ploidy and hybridity, Arabidopsis ecotypes were crossed to generate a series of reciprocal diploid, triploid, and tetraploid hybrids (Fort et al., 2016; Miller, Zhang, & Chen, 2012). Tetraploid plants displayed a lower growth rate compared with other ploidies, whereas hybrids displayed increased early stage growth rate (Fort et al., 2016). Otherwise, all hybrids, except for triploid hybrids with tetraploid mother, displayed biomass vigor compared to their respective parents (Miller et al., 2012).

Modern sugarcane cultivars are the products of hybridization with wild genotypes to improve their hardiness (Roach, 1972). These hybrids are adapted to tropical and subtropical

climates, and are vegetatively propagated. The result has been a substantial increase in sugarcane biomass and sugar content over the decades (Hoang, Furtado, Botha, Simmons, & Henry, 2015; Ming, Liu, Moore, Irvine, & Paterson, 2001). In maize, increasing ploidy of an inbred had a detrimental effect on plant height and the magnitude of hybridization at the tetraploid level is greater than for the diploids (Riddle & Birchler, 2008). Additionally, the yield potential of hybrid rice cultivars is higher than that of inbred cultivars. The hybrid rice cultivars had high grain weight and biomass accumulation at maturity (Haque, Pramanik, Biswas, Iftekharuddaula, & Hasanuzzaman, 2015; Jiang et al., 2016). Another important economic crop plant is the oil producing canola. To date, hybrid cultivars have been successfully used in agriculture due to their significant yield increase of 30 to 60% and their oil quality over the mid-parents (Grant & Beversdorf, 1985; Liu, Qian, & Meng, 2002; Sernyk & Stefansson, 1983).

miRNA

MicroRNAs (miRNAs) are a class of naturally occurring small non-coding RNA molecules about 20–22 nucleotides in length, which play essential roles in plant development and responses to environmental stresses (Borges & Martienssen, 2015). Thus, manipulation of miRNA expression levels could provide an effective strategy for improving plant biomass and one good candidate is the miR156, which is conserved in all Angiosperms (Morea et al., 2016).

MiR156 regulates members of the SQUAMOSA-PROMOTER BINDING PROTEIN-LIKE (SPL) transcription factor family, which affect the expression of downstream genes and result in the regulation of complex network involved in plant growth and development (Cardon et al., 1999). Overexpression of miR156 in Arabidopsis repressed the transcript abundance of related SPL genes, causing dwarfism and increased total leaf numbers, and biomass (Schwab et al., 2005). Alfalfa plants overexpressing miR156 had reduced internode length and stem thickness, a delay in flowering time and elevated biomass production (Aung et al., 2015). Both low and moderate levels of miR156 overexpression led to improve switchgrass biomass by 58%-101% yield (Fu et al., 2012). Transgenic plants overexpressing miR156 in poplar had shorter internode length and a reduction of 30% in stem lignin content (Rubinelli, Chuck, Li, & Meilan, 2013). In red clover, overexpression of miR156 increased number of shoots, delayed flowering, and accelerated biomass accumulation (Zheng, Liu, Goff, Dinkins, & Zhu, 2016). MiR858 is another conserved miRNA family playing an important role in regulating of several MYB transcription factors involved in flavonoid biosynthesis (Jia et al., 2015). Overexpression of miR858a in Arabidopsis led to down-regulation of MYB11, MYB12 and MYB111 transcription factors resulting to a robust growth and early flowering of transgenic plants (Sharma et al., 2016). In rice, overexpression of miR397 led to increased grain size, additional panicle branching, higher grain productivity and biomass (Zhang et al., 2013). In addition, Arabidopsis plants overexpressing miR397b develop more than two inflorescence shoots and an increased silique number, resulting in enlarged seeds and higher seed numbers (Wang et al., 2014).

Conclusion

At this moment, there is an increasing demand to develop and implement strategies for production of chemical compounds from biomass instead of using petroleum. Advances in biotechnology have led to new strategies to produce more biomass in order to supply the demand for organic matter. Since this can no longer be achieved by traditional methods alone, breeding through plant biotechnology is an imperative.

Many of the growth-promoting genes discussed above played an important function in plant development, which are relevant to crop biomass and yield (Table 1). The use of transgenic approaches will allow direct modification of plant biomass by altering specific genes. However, a current challenge is to transfer these findings to field trials and demonstrate the effects on yields. Because the genomes of model plants are less complex in their organization and regulation compared to most crops, results obtained with the later cannot be automatically applied to commercial varieties. The results obtained with model plants are fundamental to indicate potential targets, however allelic diversity, difficulties in transformation of many crops or varieties, and genetic silencing are factors that decrease the efficiency in obtaining transgenic crop lines.

Recent advances in technologies for genome editing have revolutionized molecular genetics. Unlike the gene knockdown mediated by RNAi, the CRISPR/Cas9 system technology could be utilized for the creation and use of novel allelic variants for breeding in crops (Bortesi & Fischer, 2015). This ability to produce knockout plants is fundamental to support plant scientists by enabling a rapid creation of mutations in genes where no known mutant is available (e.g. transposon insertion) (McCarty et al., 2005). However, for overexpression analysis, the constitutive promoter remains a powerful tool. Other alternative to increase biomass is the manipulation of multiple genes in plants. The stacking of different genes in plants is rapidly gaining popularity in biotech crop production for simplify downstream plant breeding and trait introgression into cultivars.

Conflicts of interest

The authors declare no conflicts of interest.

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