



Research review paper

Genetic modification of plant cell walls to enhance biomass yield and biofuel production in bioenergy crops



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ABSTRACT

Plant cell walls represent an enormous biomass resource for the generation of biofuels and chemicals. As lignocellulose property principally determines biomass recalcitrance, the genetic modification of plant cell walls has been posed as a powerful solution. Here, we review recent progress in understanding the effects of distinct cell wall polymers (cellulose, hemicelluloses, lignin, pectin, wall proteins) on the enzymatic digestibility of biomass under various physical and chemical pretreatments in herbaceous grasses, major agronomic crops and fast-growing trees. We also compare the main factors of wall polymer features, including cellulose crystallinity (CrI), hemicellulosic Xyl/Ara ratio, monolignol proportion and uronic acid level. Furthermore, the review presents the main gene candidates, such as *CesA*, *GH9*, *GH10*, *GT61*, *GT43* etc., for potential genetic cell wall modification towards enhancing both biomass yield and enzymatic saccharification in genetic mutants and transgenic plants. Regarding cell wall modification, it proposes a novel groove-like cell wall model that highlights to increase amorphous regions (density and depth) of the native cellulose microfibrils, providing a general strategy for bioenergy crop breeding and biofuel processing technology.

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Contents

1. Introduction	998
2. Effects of wall polymer features on biomass saccharification	998
2.1. Cellulose	998
2.2. Hemicelluloses.	1000
2.3. Lignin.	1005
2.4. Pectin.	1005
2.5. Wall proteins	1005
3. Genetic modification of plant cell walls	1005
3.1. Wall polymer synthesis.	1006
3.2. Wall polymer degradation	1009
3.3. Wall network construction	1010
4. Evaluation of bioenergy crop breeding	1010
4.1. Herbaceous grasses.	1010
4.2. Food crops	1010
4.3. Woody trees.	1011
5. Biotechnology of biofuel process	1011
5.1. Biomass pretreatment	1011

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5.2. Lignocellulose enzymatic hydrolysis	1011
5.3. Bioethanol fermentation	1011
6. A model for cell wall modification and biofuel application	1012
Acknowledgments	1012
References	1012

1. Introduction

Bioenergy is a renewable form of energy derived from biological sources and can be used to generate heat, electricity and fuels (Himmel and Bayer, 2009; Yuan et al., 2008). By 2050, it is estimated that the use of bioenergy must increase at least four folds to reduce worldwide CO₂ emissions by 50%. While the use of first-generation biofuels, such as starch- and sugar-derived ethanol and plant oil-derived biodiesel, has already made small but significant contributions to the global energy supply, the increase in bioenergy will most likely stem from the use of lignocellulose, which produces 1.5×10^{10} tons/year of biomass, with a 60% conversion efficiency (Chen and Peng, 2013; Pauly and Keegstra, 2008; Ragauskas et al., 2006; Rubin, 2008). Lignocellulosic ethanol, a second-generation biofuel, has the potential to fill most global transportation fuel needs and does not present a conflict between energy demand and food supply (Peng, 2012; Sims et al., 2010).

Plant cell wall represents the most abundant renewable biomass resource for biofuels on the earth. The conversion of lignocellulose to ethanol involves three major steps: physical and chemical pretreatments to enhance cell wall destruction, enzymatic digestion to release soluble sugars, and yeast fermentation to produce ethanol (Carroll and Somerville, 2009; Xu et al., 2012). Because plant cell walls have evolved a complex structure and the mechanical strength to resist physical and biochemical digestion in nature, lignocellulose recalcitrance greatly leads to an unacceptably costly biomass process (Himmel et al., 2007; Lynd et al., 2008). In principal, biomass recalcitrance is determined by cell wall composition, wall polymer characteristics, and wall polymer network structures. Hence, genetic modification of plant cell walls represents a powerful solution to biomass recalcitrance (Chen and Dixon, 2007; Demura and Ye, 2010; Torney et al., 2007; Vega-Sánchez and Ronald, 2010; Wang et al., 2014b; Xie and Peng, 2011).

The cell wall is a layer of structural material that surrounds the plant cell and extends to the protoplast (Fig. 1A, B). The plant cell wall can be divided into primary and secondary cell walls (Fig. 1C, D), which are systematically formed during plant cell growth and development (Cosgrove, 2005; Dumville and Fry, 2000; Hall and Cannon, 2002; Motose et al., 2004; Wang et al., 2014b). Plant cell walls are mainly composed of cellulose, hemicelluloses and lignin, as well as minor pectic polysaccharides and wall proteins (Fig. 1E–H), and they have distinct compositions in different plant species (Table 1). As plants comprise of numerous cell types with extremely complicated cell wall structures and diverse biological functions, the genetic modification of plant cell walls is often associated with defects in plant growth and development, which could affect important agronomic traits in crops such as plant lodging resistance, biomass yield and environmental stress tolerance (Casler et al., 2002; Li et al., 2015b; Pedersen et al., 2005; Vega-Sánchez and Ronald, 2010). It thus becomes critical to find out an optimal genetic engineering approach that not only maintains normal plant growth but also enhances biomass yield and lignocellulose enzymatic digestibility (Wang et al., 2014b; Xie and Peng, 2011). In the present review, we describe recent research progress about cell wall polymer distinct effects on biomass enzymatic saccharification under different physical and chemical pretreatments in various plant species, including herbaceous grasses of high biomass yield (*Miscanthus*, switchgrass, and reed), major food crops (rice, wheat, maize, sweet sorghum, and cotton) with large biomass residues, and fast-growing

woody trees rich in cellulose. We then discuss the key genes involved in cell wall modifications that might enhance both biomass yield and biofuel production. Finally, we present a hypothetical model for bridging plant cell wall engineering and biomass processing technology.

2. Effects of wall polymer features on biomass saccharification

Plant cell wall composition is highly variable among different plant cell types and tissues. It therefore remains technically challenging to identify individual wall polymers that impact the enzymatic digestibility of biomass. For example, selection of one genetic mutant or a one-gene transgenic plant could result in multiple wall polymer alterations. However, based on systems biology analyses of large populations of biomass samples, three major wall polymers (cellulose, hemicelluloses, and lignin) have been characterized in several plants used primarily for biofuel production, as shown in Table 2 and Fig. 2. In addition, we discuss recent studies of pectin and wall proteins in this section.

2.1. Cellulose

Cellulose is a major component of plant cell walls that accounts for approximately 2–4% of cereal endosperm walls to 95% of the secondary cell walls of cotton fibers (Delmer, 1999; Huang et al., 2015b; Li et al., 2013a; Ragauskas et al., 2006). Among herbaceous grasses, *Miscanthus* accessions exhibit a large variation in cellulose levels, from 20% to 46% (Huang et al., 2012; Magid et al., 2004; Meineke et al., 2014), whereas switchgrass and reed have cellulose levels of approximately 32–39% (David and Ragauskas, 2010; Lindsey et al., 2013). In agronomic crops, cellulose variation has been observed among rice genetic mutants (Li et al., 2015b), sweet sorghum germplasms (Li et al., 2014a; Wu et al., 2015), maize and wheat cultivars (Chundawat et al., 2007; Jia et al., 2014; Wu et al., 2014b), and cotton and rapeseeds varieties (Huang et al., 2015b). By comparison, economical crops (e.g., ramie, jute, kenaf, and agave) and woody trees (e.g., poplar and pinus) are extremely rich in cellulose, with levels ranging from 42% to 80% (Escamilla-Treviño, 2012; Leple et al., 2007; Vieira et al., 2002).

Cellulose is a high molecular weight polymer found in plant cell walls that is composed of β -1,4-glucan chains. Intermolecular hydrogen bonding between these parallel chains leads to a compact cellulose structure that is crystalline, fibrous, and mechanically strong (Brown and Emsley, 2004). Cellulose crystallinity is thus a key feature of cell walls that not only accounts for the amorphous and crystalline regions of native cellulose but also reflects cellulose interactions with other wall polymers (Kaida et al., 2009). Using X-ray diffraction, the crystalline index (CrI) has been applied to detect cellulose crystallinity in various biomass materials (Bansal et al., 2010; Park et al., 2010). Cellulose CrI has thereby been determined to be a primary negative factor on biomass enzymatic digestibility under various physical and chemical pretreatments in almost all plant species examined (Zhang et al., 2013). Recently, Li et al. (2015b) have reported that cellulose CrI is the major factor negatively affecting rice lodging resistance, a major agronomic trait significantly associated with grain yield and biomass production in crops. In addition, the cellulose level is known to have a negative impact on biomass enzymatic saccharification in most plant species examined, likely due to its positive correlation with cellulose CrI (Table 2).

The degree of polymerization (DP) is another important feature of cellulose that is highly variable among different plant species (Hallac

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