Chapter

Breeding Rice for Sustainable Bioenergy Production

Manasi Dash, Abinash Mishra and Mahendra Kumar Mohanty

Abstract

Bioenergy including biofuels from lignocellulosic biomass has immense potential to meet growing energy demand of the ever-growing world population. Bioenergy will help to mitigate the environmental problems arising due to burning of fossil fuels. Rice is the staple food for more than half of the world population and is grown in more than 100 countries. Rice straw is rich in lignocellulose and several technologies are available for efficient extraction and conversion of cellulose to ethanol. Thus, the surplus rice straw can be utilised to produce biofuel, so as to replace conventional fossil fuel sources. But it is reported that the present-day rice varieties showing high lignocellulosic straw biomass have low grain yield potential. Hence, it is important to re orient the breeding strategies for developing dual purpose rice varieties that are bioenergy efficient without compromising grain yield.

Keywords: Rice, Bioenergy, Cellulose, Lignin, Cell wall architecture, Genomics, QTLs

1. Introduction

After the Paris climate change agreement in 2016, its signatories are making considerable efforts towards reducing carbon emissions into the atmosphere. Production of biofuel also called as 'green energy' will be a key target to achieve this by reducing the use of petrochemicals. Now focus is to harness ethanol from the existing ample quantity of lignocellulosic feedstocks such as rice and wheat straws, which are usually burnt in the fields thereby causing air pollution and health hazards [1]. The bioenergy crops have tremendous potential to address the twin issues of climate change and energy security by eliminating the 'food verses fuel' disputes.

Of the various crops grown worldwide, rice has an immense potential to be used as a dual-purpose crop, due to it's wide geographical distribution, covering entire tropical, subtropical and Mediterranean region of the globe [2]. High amount of cellulose (32–47%) and hemicellulose (19–27%) in rice straw, which can be converted to biofuel, has made it a potential future bioenergy crop [3–6]. But the cell wall polymers (cellulose, hemicellulose and lignin) form a complex network by crosslinking with each other. Hence, various pre-treatments are employed in order to break this complex to ensure higher amount of cellulose availability for the activity of cellulosic enzymes to yield considerable sugars. These pre-treatments are costly and environment unfriendly, so various genetic approaches can be utilised to enhance cellulose availability. Lignin, comprising three main types of monolignols, serves as a promising target to

alter the cell wall architecture in different ways in rice [7–9]. Cellulose synthases genes particularly, OsCesA4, OsCesA7 and OsCesA9, associating with specific phenotypes, can also be suitably engineered to enhance cellulose content without changing lignin and other polymers in cell wall [10]. So, breeding approaches that can alter plant cell wall architecture can be used to develop bioenergy efficient rice variety but, subjected to one condition that it should not affect yield contributing traits negatively.

Usually, a negative correlation has been observed between grain yield and biomass traits. Breeding for high grain yield is associated with developing cultivars with reduced plant height and short leaves and thereby, reducing the plant biomass as a whole. The plant breeding strategies have to be reoriented towards selection of higher yielding plants with moderate biomass traits including lesser ash & potassium content in vegetative biomass. Also, the role of stay green traits, fostering greater decomposition of vegetative biomass as well as rewarding higher yield, can never be underestimated in this regard. This chapter will deal with the above said issues and measures, with the prime focus on methods for developing rice genotypes for higher yield and greater biofuel production, in subsequent heads.

2. Ethanol production from rice straw

Ethanol production is primarily centered around the lignocellulosic fraction of the plant biomass. Among all the left-over waste of crop species, rice straw is the cheapest and most abundant source of lignocellulosic feed stock. Rice straw, possessing considerable amount of cellulose (32–47%), hemicellulose (19–27%), with relatively less lignin (5–24%), is considered as one of the potent bioenergy sources [3, 5]. Various enzymes have been identified in the biosynthesis of these polymers (**Figures 1-3**) which determine the type and amount of polymer production in the plant cells. The cell wall polymers form a complex network by crosslinking with each other inside the cell walls. Hence, various pre-treatments are employed in order to break these complexes, to reduce crystallinity of cellulose (crt), degree of polymerisation (DP), increase in

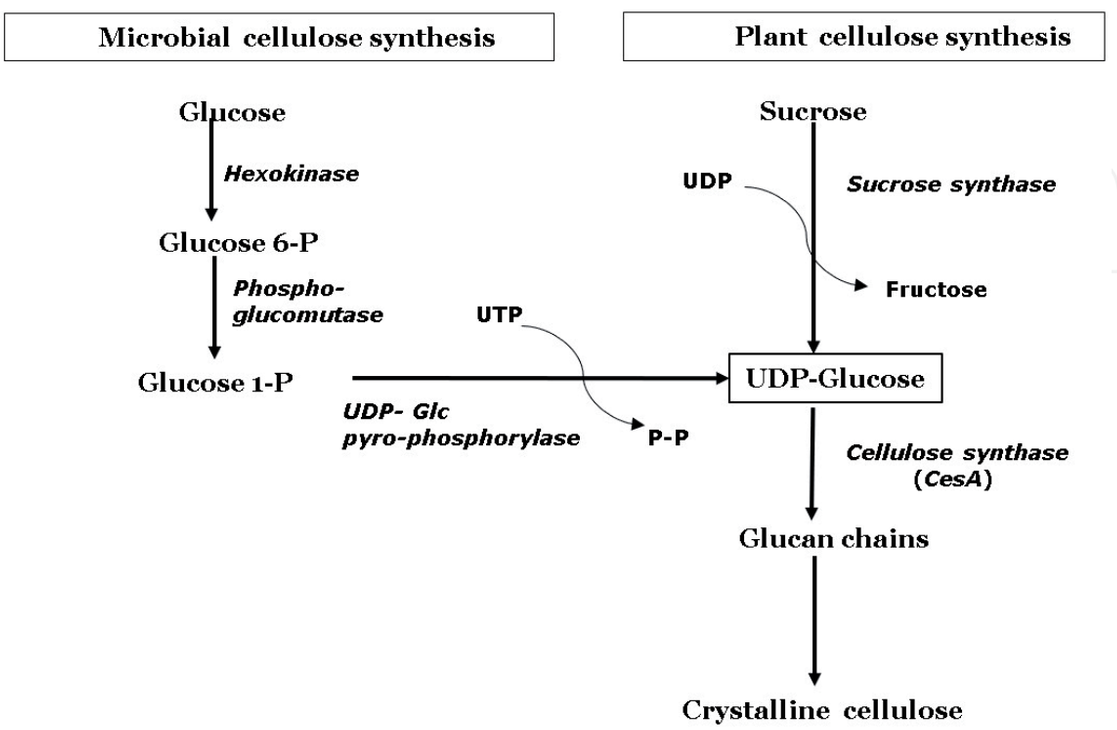

Figure 1.
Cellulose biosynthesis pathway in microbes and plants.

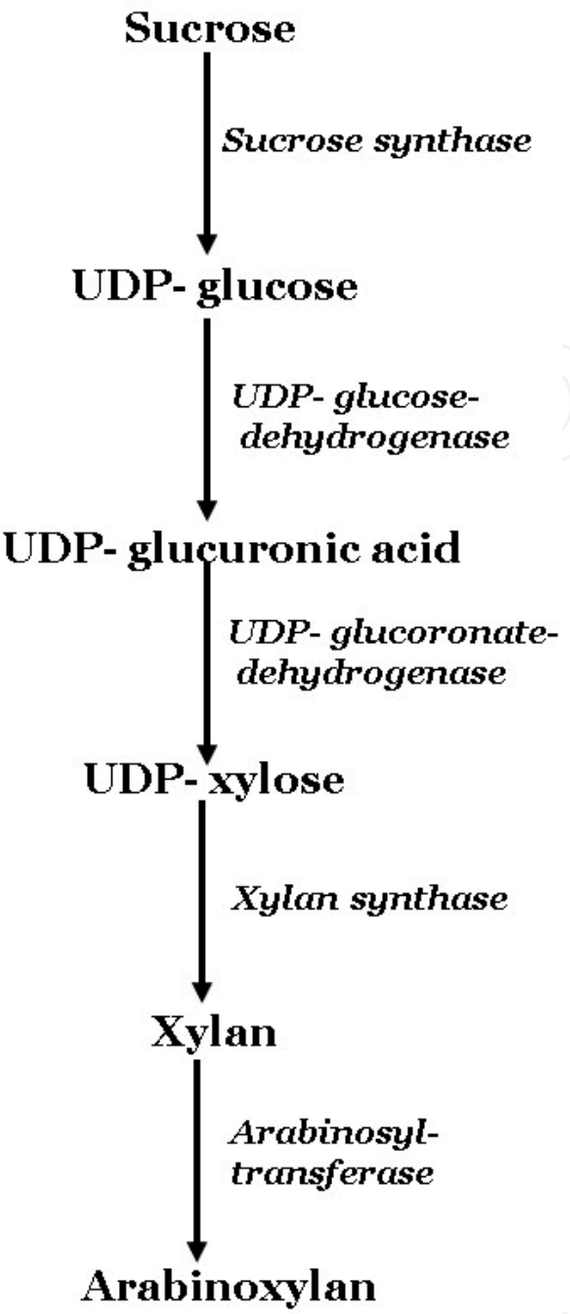

Figure 2.
Hemicellulose monomer biosynthesis pathway.

biomass surface area, and breaking the lignin seal. Chemical pre-treatment of rice straw is practiced to enable enzymatic saccharification for ethanol production [13–26].

Biological pretreatment, an eco-friendly method, overcomes the disadvantages of chemical pretreatment. White-rot fungi (*Pleurotus ostreatus*) of class Basidiomycetes are most promising microorganisms [27]. Basidiomycetes degrades lignin fraction in lignocellulosic biomass in rice straw. Patel and co-workers [28] in a study on rice straw reported that pretreatment involving *Aspergillus niger* and *Aspergillus awamori*, followed by *Saccharomyces cerevisiae* aided fermentation and recorded highest ethanol yield of 2.2 g/l. Cellulose upon hydrolysis produces glucose while hemicellulose produces hexose and pentoses [29]. Use of steam pretreatment or hydrolysis of rice straw using H_2SO_4 has also been reported [30, 31]. Pretreatment with *Aspergillus niger* increased the glucose yield from 43 to 87% [32].

Cellulose contain glucans while hemicellulose is composed of polymers of xylan, mannan, glucan, galactan and arabinan. The general process of ethanol

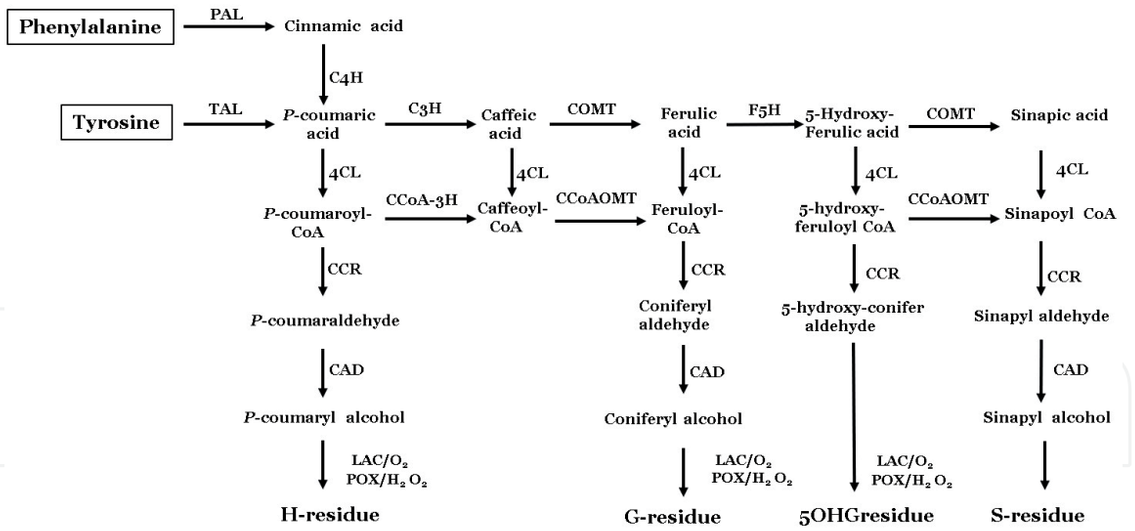

Figure 3.
Lignin biosynthesis pathways. The various enzymes are PAL [phenylalanine ammonia-lyase]; TAL [tyrosine ammonia-lyase]; C4H [cinnamate 4-hydroxylase]; C3H [4-hydroxycinnamate 3-hydroxylase]; COMT [caffeic acid 3-O- methyltransferase]; F5H [ferulate 5-hydroxylase]; 4CL [4-coumarate: CoA ligase]; CCoA-3H [coumaroyl-CoA 3-hydroxylase]; CCoAOMT [caffeoyl-CoA O-methyltransferase]; CCR [cinnamoyl-CoA reductase]; CAD [cinnamyl alcohol dehydrogenase]; LAC [laccase]; and PDX [peroxidase] (modified from Furtado et al. [11]; Vermerris and Abril [12]).

production involves conversion of cellobiose to ethanol by a series of steps of involving pre-treatment, enzymatic saccharification and fermentation as described earlier. These steps may include simultaneous saccharification and fermentation (SSF) or separate enzymatic hydrolysis and fermentation (SHF). SSF is generally used as cost incurred in the process is less [33]. In this process also, higher yield of ethanol is obtained. However, some drawbacks are observed in this process such as requirement of optimum temperature (40-50°C) for enzymatic hydrolysis, which the microorganisms cannot tolerate. This problem can be tackled by using thermophilic microorganisms such as *Kluyveromyces marxianus, Candida lusitamiae and Zymomonas mobilos* or mixed culture of *Bettanomyces clausenii* and *Saccharomyces cereviseae* [34, 35]. Shengdong and co-workers [36] employed the SSF of alkali and alkali/microwave pretreatment to generate ethanol using cellulase from *Trichoderma reesei* and *Saccharomyces cereviseae*. The ethanol concentration was 29.1 g/l and yield were 61.3% under optimum condition. Chada and co-workers [37] mentioned that SSF was superior to traditional saccharification in production of ethanol as it can improve the ethanol content by removal of end product inhibition by saccharification process. In the fermentation process alcohol is mixed with the straw to produce fermentable sugars and this is referred to as mash. This mash is fed into fractional distillation unit which differentiates alcohol from other components. The alcohol thus produced is cleaned and dehydrated to remove the water content. After cleaning and drying bioethanol is produced with a purity of 99.7% V/V.

These chemical processes for saccharification are harmful to the environment. Hence now research should be focused towards minimising or eliminating these steps by developing rice genotypes with higher saccharification efficiency (SE).

3. Role of plant breeding and biotechnology to enhance SE

As mentioned earlier the lignocellulosic biomass is primarily a complex network of various cellular constituents including cellulose, hemicellulose, lignin and interaction of a wide array of compounds like chlorophyll, waxes, oils, terpenes

and phenolics, called extractives [38, 39]. It is beneficial to have knowledge on the genetics as well as correlation between biomass traits and these cellular constituents. A greater insight into the composition, structure and the synthesis of cellular constituents will help in designing suitable breeding strategies for the genetic modification of cell wall architecture and in turn development of high energy efficient rice genotypes.

3.1 Morphological and biochemical characterisation of biomass traits

In simple term, it refers to the study of various morphological, physiological, biochemical traits, associated with grain and biomass yield. Rigorous phenotyping is essential for the success of any crop improvement programme. In breeding for biofuel, although some noticeable work has been done in case of bioenergy crops like sorghum, maize and sugarcane, very limited information is available with respect to rice, which is considered as a hinderance in effective phenotyping in this regard.

It is reported that culm length, stem girth, tiller length and diameter, leaf characteristics such as leaf length, width and angle as well as leaf, stem, tiller dry weight are few key biomass traits that can be used for indirect selection [40, 41]. These traits recorded at different developmental stages will help to decipher the genetic basis of biomass partitioning and accumulation in vegetative parts.

Biochemical characterisation of rice straw cell wall polymers (cellulose, lignin and hemicellulose) is an integral part of biomass phenotyping. Many methods like use of ultrasonicator, HPLC, microarrays, Infrared absorption spectroscopy, X- ray diffraction (XRD), transmission electron microscopy (TEM) and carbon-13 nuclear magnetic resonance (C-NMR) spectroscopy can be used for quantitative estimation of cell wall polymers [42, 43].

3.2 Polymer composition of rice biomass

Cellulose is the utmost abundant organic compound available on earth. It is a linear polymer of repeating units of cellobiose molecule. Cellobiose, a β (1–4)-linked residue, is produced when two glucose molecules (one in 180 deg. rotation) are in proximity to yield a β (1–4)-linkage. These cellulose fibres impart a greater rigidity and strength to the cell wall and hence, enabling plants to exhibit a wide spectrum resistance to various biotic and abiotic factors [12]. The non-cellulosic polysaccharides further enhance the rigidity and strength of plant cell walls by cross-linking with cellulose and lignin. Various reports have suggested this cellular constituent as a mixture of various monosaccharides such as xylose, arabinose, glucose, galactose and rhamnose as well as certain acids [44, 45]. This complex nature of non-cellulosic polysaccharides as well as their involvement in cross linking with cellulose, possesses a major setback in the efficient enzymatic degradation of cellulose to produce biofuel.

Lignin, the second most abundant biopolymer after cellulose, is polymerised with three main types of monolignols namely, Syringyl alcohol (S), Coniferyl alcohol (H) and p-Coumaryl alcohol (H) [46, 47]. As a complex phenolic compound, it improves cell wall rigidity and strength, imparts resistance to a wide array of microbes [48], fosters transporting of minerals through vascular bundles [49], involves in resistance against lodging as well as abiotic anomalies [50–52].

Cellulose and hemicellulose in rice straw can be subjected to fermentation for production of biofuels. However, their efficient conversion into fermentable sugars is hindered by presence of higher amount of lignin (5–24%), ash (10–17%), silica (75% of ash) and potassium [53].

In rice, silica comprises 74.67% of the stem ash content. Both high ash and high silica (SiO2) silica content of ash negatively affect biochemical conversion of lignocellulosic feedstock [11, 53]. High silica content reduces the availability of cellulose to enzymatic digestion and thus, reducing saccharification efficiency. Besides this, high silica accumulation in the cell walls disrupts the cellulosic microfibrils and such aberration hinders overall sugar release and ultimately, ethanol yields in subsequent stages. Therefore, considerable efforts are required to engineer silica content along with lignin and non-carbohydrate polysaccharides content to develop rice genotypes, amenable to greater enzymatic digestibility.

Although, different enzymatic and chemical pre-treatment methods are being employed for the disruption of this complex network but these procedures are energy intensive, costly and harmful to the environment. Hence, genetically modifying the cell wall architecture by employing conventional and modern breeding methods are beneficial for sustainable biofuel production [11, 54].

3.3 Modifications in polymer composition for elevating cellulose utilisation

As discussed earlier, lignin serves as a key element in cross linking of cellulose and hemicellulosic polysaccharides. This feature is beneficial to the rice plant as it helps it to counteract biotic and abiotic stress but it is a limiting feature for biofuel production. The cross linking creates a barrier for the cellulose degrading enzymes to freely access cellulose for conversion. So, efforts are being made towards reducing the degree of lignification and cross linking through various approaches so as to enhance the efficiency of cellulose degrading enzymes.

3.3.1 Modification of lignin

Some noticeable work has been done to alter the plant cell wall architecture with the help of biotechnology in model dicot plants such as Arabidopsis and tobacco (**Table 1**). The purpose behind these experiments has been the downregulation of key genes involved in monolignol biosynthesis, as well as the essential enzymes involving in polymerisation thereof. Nearly 40% reduction in total lignin content was achieved by downregulating laccases and peroxidases in the Arabidopsis [61] and tobacco mutants [62], respectively. So, these available reports documenting successful reduction of lignin composition in model dicot plants can be judiciously used by the researchers to favourably alter the cell wall architecture of the less exploited prospective biofuel crops such as rice. The *japonica* rice 'Nipponbare' harbouring an Arabidopsis TF (SHN), was found to be deficient in total lignin content. Expression of essential genes such as *CAD* (cinnamyl alcohol dehydrogenase) and 4-CL (4- coumarate- CoA ligase) were reported to be repressed, which might have contributed in producing lower lignin content [9].

Alternatively, there is another way of altering the plant cell wall architecture, by curbing the expression of essential genes involved in lignin monomers synthesis (**Figure 3**). In rice, flexible culm (*fc1*) mutant with repressed *CAD* gene, a cinnamyl alcohol dehydrogenase gene, was reported to synthesise reduced level of H and G lignin monomers [7]. Zhang and co-workers, [60] were able to produce some transgenics with improved saccharification efficiency as compared to wildtype by targeting same *OsCAD2* gene in rice. Apart from these genes, few other genes including caffeoyl-CoA- methyl transferase (*CCoAOMT*) and caffeic acid o-methyl transferase (*COMT*) were genetically engineered in different species such as alfalfa, canola, maize, poplar, tobacco and sugarcane, to alter the lignin monomers composition [63–66, 70–74]. Several reports enumerating the modifications of some key TFs such as *OsMYB103L* are also available for improved plant architecture in rice [58, 59].

Cell wall polymer regulation	Genes	Approach	Phenotypes	Reference(s)
Cellulose synthesis	*OsCesA4*	Bc11 (G858R), NE1031, ND5658 (TOS17)	Reduce cellulose; affect growth	[10]
	OsCesA7	NC0258, ND8759 (TOS17)	Reduce cellulose; affect growth	[10]
	OsCesA9	ND2359 (TOS17)	Reduce cellulose; affect growth	[10]
	OsGH9B	Osfc4; Osfc11 (T-DNA)	Reduced Cr1(Cellulose crystallinity)	[55]
	OsGH9B 1; OsGH9B 3	pCAMBIAI11300: *OsGH9B*	Reduced Cr1; DP (Degree of Polymerisation)	[56]
	Fc17 (OsCESA4)	F_2 (fc17 × MH 63)	Reduced Cr1	[57]
Cellulose regulation	*OsMYB103L*	pUbi:: OsMYB103L (OE)	Increased secondary cell wall	[58]
	OsMYB103L: NAC29,31	pUbi:: OsMYB61; NAC29, 31 (OE)	Increased secondary cell wall	[59]
Lignin synthesis	*OsCAD2*	CRISPR/Cas9	Altered H and G residues; reduced lignin	[60]
	Fc1 (Cinnamyl-alcohol dehydrogenase)	Fc1 (T-DNA)	Reduced H and G residues; reduced lignin	[8]
	4CL; CAD	p35S::AtSHN2 (OE)	Reduced lignin	[9]
	Bc1 (COBRA like protein)	bc1 ($_{\gamma}$-rays)	Reduced lignin	[7]
	Laccases	LAC4/LAC7 (T- DNA)	Reduced lignin; hinderance in deposition of G subunits	[61]
	Peroxidases	TP60 (RNAi)	Reduced lignin; reduced G and S residues	[62]
	COMT	pWFOsC4H::Bg4CLi (RNAi)	Reduced lignin; reduced S/G ratio	[63]
	CCoAOMT	*CCoAOMT (RNAi)*	Altered lignin subunit composition	[64–66]
Hemicellulose synthesis	*OsXAX1 (GT61)*	axa1 (T-DNA)	Reduced xylose, ferulic acid, coumaric acid	[67]
	BAHD acetyl transferase	pUbi: OsAt10	Reduction in matrix bound ferulic acid	[68]
	OsIRX10 (GT47)	*OsIRX10* (RGT6229D)	Reduced X/A; affect growth	[69]

Table 1.
Candidate genes for preferable altering the cell wall polymers (cellulose, hemicellulose and lignin) in plant system.

3.3.2 Modification of hemicellulose

A general trade-off has been discovered between saccharification efficiency and ferulic acid [75, 76]. Bartley and co-workers, [68] reported the possible role of OsAt10, a BAHD acetyltransferase gene in achieving higher sugar release by favourably modifying glucuronoarabinoxylan (GAX) in rice. Young leaf tissues of the genetically engineered plants were found to be deficient in ferulic acid (FA). The possible role of other genes such as OsXAX1 and OsIRX10 were known to reciprocate similar results in rice [67, 68].

3.4 Role of cellulose synthase genes

Cellulose synthase enzymes are pivotal for cellulose synthesis. These proteins organise to form a hexameric 'rosette' structure approx. 25–30 nm diameter [77]. The plant cellulose synthase (*Ces A*) genes were first identified during random sequencing of cotton ESTs [78] and its role in cellulose synthesis was first reported in Arabidopsis Ces *A* mutants [10, 79]. The Ces *A* gene family was also identified in rice, maize, barely and poplar [57, 80–92].

Tanaka and co-workers [10] generated four different introgressed lines, showing brittle culm phenotypes by suitably introgressing Tos17, a retroposons in the genetic background of rice wildtype. They identified three cellulose synthase genes namely, *OsCesA4*, *OsCesA7* and *OsCesA9* on three different chromosomes. The mutant *Osfc16* with a mutation on *CesA9*- conserved sequence was found with altered cellulose crystallinity (crt1), which possibly enhanced the saccharification efficiency [93]. In a similar experiment, conserved site of another potential cellulose synthase CesA4 is mutated to alter cellulose crystallinity (crt1) for enhanced cellulose synthesis in *fc17* mutants [57]. Considerable efforts have been made to alter various structural properties of cell wall constituents including cellulose crystallinity (crt1) and degree of polymerisation (DP) which usually negatively affect the saccharification potential. In this regard, some noticeable work has been done to identify and characterise few genes of glycoside hydrolase family (*OsGH9B 1, 3 and 16*), promising candidate genes for favourably modifying structural properties of cell wall polymers as well as cellulose synthesis in rice [55, 56]. Beside cellulose synthase genes, other genes including KORRIGN [94–96], COBRA-like protein [7] and KOBITO [80] need to be explored properly to develop energy efficient elite cultigens in rice.

3.5 Genomics and QTL identification for biomass traits

Correlation between biomass traits and grain yield in rice is negative. Breeding varieties for high grain yield usually involves designing the varieties for medium plant height with short erect flag leaves which in turn affect the total biomass yield. This can be addressed to some extent by crossing rice cultivars, showing high polymorphism for grain yield potential as well as biomass traits and identify the candidate genes or QTLs involved. After the successful mapping of genes or, QTLs, the linked markers can be used for marker assisted selection (MAS) as well as can be used to screen the existing wild types or landraces for dual characteristics. As we have discussed earlier, cell wall polymers i.e., cellulose, hemicellulose and lignin composition can be altered for improved saccharification traits, hence, it is essential to search for the genetic link between cell-wall polymer composition and grain yield in order to breed dual purpose rice cultigens [97–103]. Gui- Fu and co-workers [97] identified few major QTLs associated with three plant traits namely, total biomass yield, straw yield and grain yield by developing suitable doubled haploid population. A QTL co-associated with both cell wall polymer composition and heading

date (HD17) has also been identified by crossing parents with considerable polymorphism for the dual characters [102]. Recently, Genome wide association survey (GWAS) involving high throughput molecular markers (SNPs) were employed to identify the genomic regions exhibiting significant association between markers and phenotypic trait and characterise the candidate genes involved [101]. Dissecting the genomic fragments involving lignin and cellulose biosynthesis is possible now with the application of GWAS technique [100].

3.6 Plant breeding strategies for improving biomass traits

Pre- existence of variability is of paramount importance in any crop improvement programme. Selection, being the core stone of plant breeding activities, is employed to harness the existing variability present in various germplasms including wild types and landraces, before creating additional variability by mutation.

A preferred high HI for good yield reduces the vegetative biomass of the rice as a whole including reduction in plant height. There is a trade-off for plant height vs. biomass yield. Hence, the role of long- culm rice cultivars in breeding high energy efficient varieties has been given due consideration [104–108]. However, an increase in culm length may increase the risk of plant lodging, which is a major factor influencing rice grain yield stability especially in direct-seeded rice. A thick culm with tolerable lignin content in cell wall will decrease the risk of plant lodging. So, there should be a balance between the cell wall constitution and morphological characters. Hence, judicious selection of genotypes for increased plant height with thick culm along with high grain yield can address the negative impact exerted by short culm height on overall biomass production. Few researches have enumerated the importance of selecting certain traits such as stem girth, plant height, leaf, sheath and stem weight for higher biomass yield in rice [40, 108, 109].

Another way for breeding dual purpose cultigens is to incorporate 'stay green' traits in cultivated type [110, 111]. Varieties possessing these traits are able to maintain higher photosynthetic activity at post-flowering stage, increasing yield thereof. At the same time, higher decomposability of these traits could serve the dual objectives as discussed above. Hence, there is a possible opportunity to exploit this stay green character in developing dual purpose rice genotypes as it has been exploited in other biofuel/bioenergy crops. Also, this character genetically enhances the photosynthetic efficiency, there may be no need to apply extra N inputs. Nevertheless, more research is required in this aspect. As of till date there are no reports of this strategy being exploited in breeding rice varieties for dual purpose.

Next it is important to identify the genetic loci (QTL) associated with these stay green trait and the markers flanking those regions [112–115]. Various biotechnological tools can then be employed for their successful integration into the plant genome or alternatively, marker aided selection (MAS) can be employed for varietal improvement. Also, heterosis breeding can be used to exploit the possible heterotic gene combinations in remodelling the plant architecture for higher biomass yield in rice, as it has been done in sorghum which possesses similar architectural traits [116–119].

4. Conclusion

There is an urgent need to address greenhouse gas emissions (GHGs) and climate changes occurring due to rampant use of fossil fuels. Rice straw, being an abundant source of lignocellulosic feedstock, has the potential to produce green energy to address the above said global concerns. Lignin and hemicellulose

complexes act as hinderance to produce energy efficient cultigens and hence, various studies are being made to down regulate the gene involved in their biosynthesis without affecting the plant system and cellulose concentration. Directly engineering cellulose synthase genes also provides an alternative opportunity in designing plant cell wall architecture. Stay green traits and heterosis breeding enhance the opportunity of developing energy efficient varieties to a greater extent. Thus, the role of plant breeding can never be bypassed as careful selection of individuals for dual traits will be highly rewarding in achieving the goal of growing dual-purpose rice varieties.

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Conflict of interest

The authors declare no conflict of interest.

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