

REVIEW

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Biotechnology towards energy crops



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Abstract

Our world is experiencing an unprecedented surge in energy demand due to rapid economic growth and population expansion. This escalating need for energy poses a significant challenge as reliance on fossil fuels leads to severe environmental pollution. Consequently, the exploration of renewable energy sources, such as biofuels, emerges as a prudent solution to mitigate the energy crisis. The cultivation of novel crops and the implementation of advanced cultivation systems are gradually gaining traction, aiming to minimize dependence on depleting fossil fuel reserves and foster resilience to global climate change. These promising biological resources hold immense potential as bioenergy feedstocks, offering a versatile and sustainable means to meet the energy requirements of modern society on a daily basis. Biotechnology, in particular, can play a critical role in developing superior genotypes of energy crops, specifically tailored for efficient bioprocessing and subsequent utilization. By applying cutting-edge molecular techniques, a wide range of important traits can be enhanced, encompassing total biomass yield, production, quality, and resistance to different biotic and abiotic stresses. These advancements have the potential to significantly improve the efficiency, cost-effectiveness, and environmental benefits of biofuels. This comprehensive review aims to evaluate the potential of biotechnological applications in the development of advantageous bioenergy crops, spanning from feedstock enhancement to sustainable biofuel production. Furthermore, it provides compelling examples of cutting-edge research in the field, showcasing the prospects of energy crop innovation.

Keywords Biotechnology, Energy crop, Bioenergy, Renewable energy, Biomass

Introduction

The global energy demand has experienced a significant increase due to factors such as population growth and the expanding influence of industrialization, transportation and improved living standards (Yadav et al. 2019). To meet this demand, burning fossil fuels has become the primary method of energy production. However, the burning of fossil fuels gives rise to detrimental emissions in the atmosphere, such as carbon dioxide, greenhouse gases and nitrogen oxides, which contribute to environmental degradation (Yadav et al. 2019). For example, the combustion of coal emits carbon dioxide, particulate soot, and sulfur compounds, leading to soil

acidification. Additionally, generating electricity through nuclear fission requires extensive infrastructure and carries potential risks to the environment and human health (Gresshoff et al. 2017). The long-term consequences of fossil fuel usage, including land degradation and desertification of fertile soils, are becoming more evident (Karp and Shield 2008). The global impacts of these practices, such as climate change, severe weather events, and the rise of diseases linked to environmental pollution, highlight the urgent need to explore alternative energy sources (Yadav et al. 2019). Recognizing the negative environmental repercussions, society is actively searching for sustainable, cleaner energy alternatives to mitigate these challenges.

Bioenergy is a compelling solution for addressing climate change within the energy sector. Its effectiveness in mitigating climate impact varies significantly depending on the source and cultivation methods of biomass feedstocks (Correa et al. 2019). For instance, when wood

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is burned for energy, it releases carbon dioxide into the atmosphere. Nevertheless, the emission can be substantially offset if the harvested trees are promptly replaced with new trees in a well-managed forest environment. The newly planted trees would absorb carbon dioxide from the atmosphere as they grow, effectively mitigating the carbon footprint (Daley 2018). In terms of renewable energy contributions, bioenergy holds a prominent position in the transport and heating sectors, and it also plays a significant role in generating renewable electricity (Belyakov 2019). Accounting for approximately 14% of global energy demand, bioenergy harnesses the energy potential within recently living biological materials, known as biomass. Various biological materials can be converted into thermal energy, electricity, and transportation fuels (biofuels) through diverse processes. Notably, numerous established bioenergy pathways have been technologically proven, with commercially available systems already in place (Morales 2019). Furthermore, the advantages of bioenergy extend beyond environmental benefits. It can contribute to a more secure, sustainable, and economically robust future by providing domestic sources of clean energy, reducing dependence on imported oil, generating employment opportunities, and revitalizing rural areas all of which contribute to a prosperous society. By leveraging bioenergy, societies can foster energy independence, enhance environmental stewardship, and promote socio-economic development, thereby paving the way for a brighter future.

Agriculture plays a crucial role in promoting an excellent source of raw materials for the generation of sustainable bioenergy, which is renewable and ecological. Energy crops are specific plant species cultivated to generate bioenergy. These crops possess favourable characteristics such as high biomass yield, rapid growth rates, and efficient conversion of sunlight into chemical energy. Energy crops offer numerous benefits, starting with their renewable nature and ecological advantages. By utilizing crops for bioenergy production, we can effectively decrease our dependence on limited fossil fuels and alleviate the impact of greenhouse gas emissions. Additionally, energy crops contribute to rural development by creating job opportunities and supporting local economies. They also provide a sustainable waste disposal solution, as some crops can effectively utilize organic waste as feedstock for bioenergy production. The main applications of energy crops lie in the generation of biofuels such as biodiesel, bioethanol, biogas etc. which can be used as alternatives to conventional fossil fuels in transportation, heating and electricity generation. Moreover, energy crops play a vital role in achieving a more sustainable and environmentally friendly energy landscape (Nair et al. 2022).

Energy crops encompass a diverse array of plant species that are primarily cultivated to generate thermal or electrical energy and produce biofuels. These crops undergo various processing techniques to yield solid, liquid, or gaseous fuels, such as pellets, bioethanol, or biogas, which in turn drive the production of electrical power. These plants can be broadly classified into two categories: woody and herbaceous. Woody plants, including willow (Mola-Yudego and Aronsson 2008) and poplar, are part of the woody classification, while herbaceous plants like *Miscanthus x giganteus* and *Pennisetum purpureum*, commonly known as elephant grass, fall under the herbaceous category. Interestingly, despite their smaller physical stature compared to trees, herbaceous crops have been found to store approximately twice the amount of CO₂ underground when compared to woody crops, as highlighted in a study by Agostini et al. (2015). This makes them a highly valuable and abundant resource, offering a more affordable alternative to oil or coal. The cultivation of energy crops in sustainable agriculture not only proves to be cost-effective and highly productive but also contributes to soil preservation and erosion prevention. By reducing global reliance on fossil fuels, energy crops play a crucial role in curbing greenhouse gas emissions and driving the transition towards decarbonization. Moreover, energy crops align with the principles of the circular economy by facilitating the environmentally friendly reuse of natural resources. Additionally, they present significant opportunities for the establishment of new businesses and job creation, particularly in rural areas, thus fostering economic growth and vitality.

Biofuels derived from energy crops offer a sustainable and environmentally friendly option as a replacement for conventional fossil fuels, leading to a reduction in greenhouse gas emissions. In recent years, many countries have shown increasing interest in biofuels as a viable alternative. Therefore, it is crucial to assess the sustainability of this renewable resource. The utilization of biofuels presents numerous benefits, including reduced carbon dioxide gas emissions, lower costs compared to fossil fuels, and their renewability (Whitaker et al. 2018). Wood cellulose, in conjunction with biofuels, has proven to be highly efficient for stationary electricity generation. Global biofuel production experienced a remarkable 109% increase from 2008 to 2013, and this trend is expected to continue with an additional 60% growth to meet rising demand (de Siqueira et al. 2013), as cited in the Organization for Economic Co-operation and Development (OECD)/Food and Agriculture Organization (FAO). The projected escalation in energy crop usage raises concerns about its long-term sustainability. The expansion of biofuel production involves challenges related to changes in land use, ecosystem impacts, and

competition for land space between energy crops, food, and feed crops. Ideal energy crops for future bioenergy feedstocks should possess characteristics such as fast growth, high yield, and minimal energy inputs for growth and harvest (de Siqueira et al. 2013). The utilization of energy crops for energy production offers advantages due to their carbon neutrality and the diverse range of plant species that can be employed. However, it is necessary to address issues regarding cost (comparatively higher than other renewable energy sources), efficiency, and space requirements for sustained production to facilitate the widespread adoption of biofuels (Whitaker et al. 2018).

Biotechnological techniques offer a means to enhance plant yields and contribute to the production of biofuels with minimal environmental impact. In the twenty-first century, biotechnology stands out as a powerful and innovative tool for addressing energy needs while mitigating environmental risks, particularly in the realm of agricultural biotechnology. This field encompasses fundamental, applied, and adaptive research, utilizing genetic manipulation and breeding techniques to develop novel crops with desired traits. By improving crop traits and enhancing biochemical conversion techniques, biotechnology holds the potential to significantly reduce production costs associated with biofuels. One avenue of progress lies in enhancing crop yields per unit of land through genetic engineering, which involves improving adaptation to biotic and abiotic factors or selecting specific variants and breeds that yield biomass suitable for bioenergy conversion (Lynd et al. 2008). Additionally, biotechnological techniques can be employed to enhance industrial microorganisms and enzymes, engineer bioprocesses, and optimize production methods, all of which contribute to the cost-effectiveness of bioenergy production.

Sustainable biomass energy production requires careful consideration of both the environmental impact and societal acceptance of such energy sources. In the coming years, advancements in biotechnology, including genetic engineering, are likely to play a significant role in the development of novel energy crops. However, it's important to note that biotechnology offers more than just genetic modifications of plants. The field of plant genomics has made remarkable progress, which can greatly contribute to conventional breeding techniques through the application of marker-assisted breeding (MAS) (Collard and Mackill 2008). By combining DNA-derived markers with other breeding tools such as quantitative trait loci (QTL), genetic and linkage maps, high-throughput tools, and gene editing methods, the process of conventional selection can be accelerated. Marker-assisted selection techniques are widely utilized in modern breeding programs because they enhance the accuracy and efficiency

of enhancing specific traits. Thus, it is expected that genetic improvement of energy crops using molecular markers will be a dominant approach in future applications. Another biotechnological aspect that holds promise to enhance future energy crops is plant propagation methods, which includes techniques like tissue culture and plant regeneration from callus or cell suspensions, protoplasts, anthers, and microspores cultivation, as well as in vitro selection (George 2008; Margaritopoulou et al. 2016). Micropropagation has the potential to overcome reproductive isolating barriers between distantly related wild relatives.

In the present era, biotechnology has become a powerful and innovative tool for generating biofuels with minimal harm to the environment. This review seeks to evaluate the capabilities of biotechnological applications in creating a beneficial pathway that encompasses the entire process of sustainable biofuel production, starting from the development of an appropriate feedstocks. Additionally, it aims to provide real-world examples of the current cutting-edge research on energy crops through biotechnology.

Energy from crops

People's prosperity and development are closely linked to energy resources, and historically, oil consumption has played a significant role in meeting those energy demands. However, due to various factors such as geopolitical tensions, economic fluctuations, and market dynamics, the availability, prices, and demand for oil can be unstable. In light of concerns about environmental pollution, climate change, and the drawbacks associated with fossil fuels, governments have been actively promoting the development of renewable energy sources to find clean, carbon-neutral alternatives to mitigate the negative impact of traditional energy sources (Gielen et al. 2019). One such alternative that shows great promise in reducing our reliance on fossil fuels and mitigating environmental issues is biofuels. These fuels are derived from renewable plant biomass and present an opportunity to address the activities that contribute to environmental instability. In addition to their potential for reducing dependence on oil and other non-renewable resources, biofuels offer a versatile and sustainable energy source that can meet the needs of modern society in the short to medium term. While solar and wind power can be harnessed for electricity and heat production, biomass stands out due to its compatibility with existing transportation infrastructure. By utilizing biofuels, we can pave the way for a greener and more sustainable future, making a positive impact on both the environment and our energy systems. Biomass can be transformed into biofuels that can directly replace or blend with conventional

transportation fuels, allowing for a more seamless transition and utilization of existing distribution systems (Jeswani et al. 2020).

It's important to note that the development and use of biofuels also come with their own set of considerations. The sustainability of biomass production, land use implications, and potential competition with food crops are some factors that need to be carefully addressed. Nonetheless, biofuels, along with other renewable energy sources, play a crucial role in diversifying the energy mix and reducing the dependence on fossil fuels, ultimately contributing to a more sustainable future of energy. It's worth noting that the utilization of these crops for energy generation can sometimes create conflicts with food production and land usage. Sustainable practices, careful crop selection, and responsible land management are important considerations to minimize negative environmental and social impacts (Rodionova et al. 2017).

Energy crops can be categorized based on their biomass composition and the specific pathways for biofuel generation. These groups include carbohydrate crops, such as sugarcane, sugar beets, and corn, used for bioethanol production; oilseed crops like soybeans, rapeseed, sunflower, and palm, utilized for biodiesel production; and lignocellulosic crops, which consist of woody crops like poplar and willow, as well as herbaceous crops like switchgrass, miscanthus and agricultural residues. Lignocellulosic crops play a diverse range of roles, including heat and power generation and second-generation biofuel production (Fischer et al. 2010). Willow has gained recognition as a highly potential biomass crop, due to its effortless propagation and rapid growth in short rotation coppice cycles and requiring fewer fertilizers. To enhance yield without significantly increasing fertilizer and water requirements, genetic engineering techniques can be employed. The adoption of non-food domestic crops in biofuel production offers several environmental benefits, including the mitigation of greenhouse gas emissions, the promotion of soil fertility by preventing land degradation, the conservation of water quality, and the creation of enhanced wildlife habitats. The use of non-food domestic crops in the production of biofuels brings about a variety of environmental advantages, such as the decrease in greenhouse gas emissions, the enrichment of soil fertility by preventing land degradation, the safeguarding of water quality, and the establishment of improved habitats for wildlife. Moreover, there are notable economic benefits to be gained. The emergence of domestic biofuel production is expected to foster localized economic growth, particularly in bioregional sectors. The establishment of agricultural activities for biofuel feedstock production will generate employment opportunities for farmers and seasonal workers, thereby facilitating rural

economic development (Jeswani et al. 2020). Additionally, the expansion of the biofuel industry will foster the establishment of collaborative manufacturing and retailing cooperatives, fostering a sense of community and shared economic growth. Moreover, this growth will also stimulate the demand for highly skilled professionals in technology development and engineering, creating new job opportunities and driving innovation in these fields.

Biofuel feedstock

Biofuel feedstocks are the raw materials used to produce biofuels. They can come from a variety of sources, including crops, agricultural residues, and algae. The specific feedstock used depends on the type of biofuel being produced. For biofuels like ethanol, feedstocks that contain starch or sugars are used (Umakanth et al. 2022). Crops such as corn, sugarcane, and wheat can be converted into ethanol through processes like fermentation and distillation. Other biofuels, such as biodiesel, are produced from feedstocks that contain oils. These oils can be extracted from crops like soybeans, canola, or palm, and then processed to create biodiesel (Malode et al. 2021). Moreover, in addition to traditional crops, the biomass derived from corn stover and sugarcane bagasse can be effectively harnessed as feedstocks to generate biofuels. Furthermore, algae are being explored as a promising feedstock for biofuel generation. Algae can produce oils that can be converted into biodiesel or can be used directly to produce biofuels through processes like pyrolysis or hydrothermal liquefaction (Ullmann et al. 2021).

One of the concerns regarding biofuel production is that some of the crops used as feedstocks, such as corn, sugarcane, and soybeans, are indeed food crops or have alternative uses for human consumption or. The utilization of food crops as biofuel feedstocks has been a topic of debate because it can potentially impact food availability and prices (Singh et al. 2023). When crops are diverted to biofuel production, it can reduce the overall supply of those crops for food or animal feed, potentially leading to higher prices or competition for resources. To address these concerns, there has been a shift towards using non-food-based feedstocks for the generation of biofuels. These agricultural residues include corn stover (stalks, leaves, and husks left after harvest), wheat straw, and sugarcane bagasse, which are abundant and readily available after the main crop harvest. Additionally, research is being conducted on the use of algae as a feedstock for biofuels, as it doesn't compete with food production and can be grown in non-arable land or even wastewater (Ullmann et al. 2021). Therefore, there is a need to strike a balance between using biofuel feedstocks that do not compete with food production and ensuring sustainable and efficient biofuel production to mitigate

the environmental impact of fossil fuels. Policies and regulations are in place in many countries to manage the use of biofuel feedstocks and encourage the advancement of biofuels that utilize non-food and non-feed-based feedstocks or waste materials.

The recognition of the immense advantages offered by non-food crops in biofuel production necessitates the integration of advanced biotechnological techniques. Biotechnology assumes a crucial role in advancing innovation and expediting the identification, stabilization, and dissemination of exceptional energy crop varieties. Moreover, it has the potential to nurture the production of valuable fuel compounds derived from plant biomass.

Biotechnological tools for the improvement of energy crops

Plants are commonly cultivated to obtain food and feed, and traditional breeding methods as well as genetic engineering have been utilized to develop plant varieties with desired characteristics (Baenziger et al. 2006). These efforts primarily aim to enhance crop productivity and quality. Moreover, there is an increasing interest in modifying food crops for the generation of bioenergy by altering their genotypes to increase starch content and achieve a higher C: N ratio. The viability of bioenergy crops depends on various factors such as germination, rapid growth and development, high yield and tolerance to different environmental stresses (Pandey et al. 2018). Consequently, the continuous pursuit of new technologies to improve the yield of bioenergy crops is highly valued. One notable advancement in this field is the application of biotechnology to enhance the overall biomass of bioenergy crops by promoting germination (Lin et al. 2009) or facilitating plant growth and development (Sheykhabglou et al. 2010; Khodakovskaya et al. 2011). It is essential to emphasize that genetic enhancement of bioenergy crops via biotechnology will play a critical role in advancing biofuel generation and promoting sustainability and environmental friendliness (Gressel 2008; Vega-Sanchez and Ronald 2010; Harfouche et al. 2011). Several ways in which advanced biotechnological applications can contribute to biofuel production are as follows.

Genetic engineering

Biotechnology allows scientists to manipulate the genetic makeup of plants to enhance their characteristics for biofuel production. This includes improving traits such as biomass yield, stress tolerance, and composition of plant biomass to maximize energy content. Enhancing the traits of bioenergy crops can be achieved by identifying natural variations (exploration of inherent variance) and genetic modifications (alteration) leading to

the development of transgenic plant varieties (Gressel 2008). These genetically altered bioenergy plants exhibit improved resilience in challenging conditions, accelerated growth rates, and enhanced caloric content.

Incorporating novel genes into plants involves employing various delivery techniques such as recombination, gene gun-mediated particle bombardment, and the utilization of *Agrobacterium tumefaciens*. Recombination enables the integration of genes into the plant's chromosomal DNA, while the gene gun exerts pressure to forcefully introduce genes into the cell. *A. tumefaciens* facilitates the entry of genes into the nucleus and their fusion with the host DNA, offering a precise transformation of plant cells. Although naturally occurring in dicot species, specific strains of *A. tumefaciens* can infect monocots like maize, sorghum, and switchgrass (Sticklen 2008). To regulate the expression of genes, a promoter is employed to control tissue-specific and inducible gene expression. The inclusion of a selectable marker in the vector aids in the identification and regeneration of genetically modified plants (Skinner et al. 2004). Selectable markers include GUS and GFP, as well as those conferring resistance to antibiotics. The evaluation of gene expression levels in a particular species assists in comprehending the impact of specific genes on desirable phenotypic traits. Techniques such as PCR, Southern blotting, and progeny analysis confirm the successful integration of transgenes. Genomics expedites the selection of desired traits compared to traditional breeding methods. Tissue culture techniques, including somaclonal variation, present opportunities for the development of new germplasm that better caters to end-user demands and enhances plant adaptability to unfavourable conditions (Schroder et al. 2008; Heaton et al. 2008).

In addition to enhancing biofuel production efficiency and reducing operational costs, the utilization of genetically enhanced organisms plays a pivotal role, complementing the genetic improvements made in bioenergy crops. A prime illustration of this lies in the development of a recombinant strain of *S. cerevisiae*, which enables the simultaneous fermentation of glucose and xylose. This genetic modification significantly improves ethanol production efficiency. Furthermore, the genetically modified strain *Z. mobilis* CP4 exhibits the remarkable ability to produce up to 95% ethanol and effectively utilizes a mixture of glucose and xylose as a substrate. Another avenue of exploration involves the overexpression of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) genes in *E. coli*, resulting in the production of high alcohol content. Notably, the *E. coli* strain ATCC11303 (*E. coli*) strain B has shown great promise as a host for incorporating the PET vector, leading to the production of over 1000 mM ethanol from hemicellulose hydrolysate sugars

(Lu and Mosier 2008). These advancements serve as compelling evidence for the immense potential of genetically improved organisms in increasing the efficiency and cost-effectiveness of ethanol production processes.

Incorporating enzymes like cellulase directly into plants offers a significant advantage over relying solely on microorganisms, as it reduces the energy input needed for production, as mentioned by Sticklen (2008). These hydrolytic enzymes, which are mostly derived from microbes, require specific genetic modifications to be suitable for expression in plants. It is crucial to ensure proper protein folding for their effective expression. However, this challenge can be overcome by targeting the enzymes to accumulate in subcellular components instead of the cytosol. By extracting these enzymes from plants, researchers can utilize them as part of the plant's total soluble protein (TSP) to convert biomass into sugars, which is compatible with traditional cellulosic ethanol production. However, further research is required to improve the production levels and enhance the biological activity of these foreign enzymes. Another area of investigation focuses on incorporating heat-induced enzymes into plants to enhance the efficiency of biomass conversion. An example of such an enzyme is *Acidothermus cellulolyticus cellulase E1*, as demonstrated by Yuan et al. (2008).

Lignin plays a vital role in providing structural support to crops, preventing lodging, and facilitating water transport through the xylem, while also offering protection against pathogens (Tew and Cobill 2008; Torney et al. 2007). However, the presence of lignin in plant cell walls poses challenges during the harvesting process and increases the cost of pretreatment (Sticklen 2008; Yuan et al. 2008). To address this issue, researchers have focused on reducing lignin production through genetic modifications. For example, studies have demonstrated that downregulating the expression of cinnamyl alcohol dehydrogenase (CAD) in poplar trees enhances the solubility of lignin in alkaline solutions, improving the efficiency of delignification (Abramson et al. 2010; Harfouche et al. 2011). This approach leads to a more uniform cell wall composition, potentially reducing the amount of pretreatment required. Furthermore, redirecting carbon flow from lignin production to overall biomass accumulation, as observed when downregulating 4-coumarate CoA ligase (4CL) in aspen trees, enhances the release of sugars during enzymatic hydrolysis. While further research is needed in the field of bioenergy crops and lignin biosynthesis downregulation, these advancements hold promise in reducing pretreatment expenses (Sticklen 2008).

The acceptance of genetically modified (GM) feedstocks for bioenergy production has faced challenges

due to concerns and scrutiny from a range of stakeholders, including environmental organizations, consumer advocacy groups, and the scientific community (Chapotin and Wolt 2007). These entities express worries about the safety of GM crops for health and the environment, as well as considering socioeconomic factors. Given that biofuels are presented as a more environmentally sustainable alternative to petroleum, they are held to higher environmental standards. Consequently, concerns surrounding genetic engineering have the potential to impede the widespread adoption of GM crops. The public's perception of GM crops has been influenced by various incidents related to agricultural biotechnology, such as the StarLink™ corn controversy, instances of pharmaceutical plants mixing with food crops, unapproved GM rice, and the impact of *Bt* corn on monarch butterflies.

Enhancing the ability of plants to thrive in challenging environments is crucial for the expansion of land utilization and the promotion of biofuel production. This necessitates the improvement of their resistance to both biotic and abiotic stresses. Schroder et al. (2008) emphasize the pivotal role of reactive oxygen species (ROS) as crucial signalling molecules that regulate gene expression, a fundamental component of plant adaptation. ROS, however, possess high toxicity due to their potential to react with various cellular components, including lipids, proteins, and nucleic acids. When plants encounter stress conditions, they experience elevated ROS production. Nevertheless, plants have developed mechanisms to effectively manage ROS levels through the expression of diverse enzymatic and non-enzymatic reactions (Schroder et al. 2008). These mechanisms involve the activity of specific enzymes and proteins, such as superoxide dismutase (SOD), ascorbate peroxidase (APOD), catalase (CAT), glutathione S-transferase (GST), guaiacol peroxidase (GPOD), enzymes associated with the ascorbate–glutathione pathway, dehydrin, actin, and histone. By expressing these enzymes and proteins, plants can effectively scavenge and neutralize ROS, thereby reducing the damage caused by oxidative stress. This enhanced antioxidant capacity allows plants to better adapt to adverse environmental conditions and survive in otherwise inhospitable habitats (Schroder et al. 2008).

Genetic engineering has been utilized to enhance energy crops for the production of biofuels. In the case of corn, natural variations known as brown midrib (*bm1*, *bm2*, *bm3*, *bm4*) induce changes in the concentration and composition of lignin within the plant (de Leon and Coors 2008). The *bm1* mutation influences the expression of CAD, while *bm2* plants exhibit reduced lignin levels and decreased ferulic acid ether content (Barriere et al. 2004). The *bm3* allele is particularly effective in improving the digestibility of the cell wall. Furthermore,

the introduction of the *Lfy1* gene trait in corn hybrids boosts forage yields by stimulating the growth of additional nodes and leaves on the main stalk and altering lateral branch development to increase biomass. Sugarcane has also undergone genetic transformation to confer traits such as herbicide resistance, disease resistance, pest resistance, and modifications in metabolomics. Field trials have been conducted on transgenic sugarcane with herbicide resistance and resistance to the Sugar Cane Mosaic Potty virus (Lakshmanan et al. 2005). Recent advancements in genetic engineering for sugarcane aim to modify sucrose metabolism to enhance sucrose production. In the case of sorghum, there are four known genes (dwarf 1–4) (*dw* 1–4 genes) that impact plant height (McQualter et al. 2004). These genes have cumulative effects on plant height, with plants carrying multiple dwarfing genes being taller than those with only one gene (meaning a plant with *dw1*, 2, and 3 would be taller than a plant with *dw1* alone). The adaptation of sorghum to long days in temperate regions led to the identification of Maturity (*Ma*) genes, with *Ma1* playing a role in controlling the rate of maturity and rendering the plant unaffected by the photoperiod. Increasing sorghum yield relies on adjusting the balance between source and sink, and drought-resistant sorghum maintains a higher photosynthetic rate under low-water conditions. The *Alt_{sb}* gene locus provides aluminium tolerance in sorghum (Saballos 2008).

In addition to the aforementioned crops, active research and development have been focused on genetically transforming crops like soybean, canola, jatropha, and camelina for biofuel production. These crops have garnered interest due to their high oil content and potential as feedstocks for biofuel manufacturing. Soybean and canola, already widely cultivated for their oil-rich seeds, can be processed into biodiesel. However, ongoing efforts aim to genetically modify these crops to enhance their oil content, improve agronomic traits, and optimize their suitability for biofuel production. Researchers are specifically targeting traits such as increasing oil yield, modifying fatty acid composition to enhance fuel properties, and improving tolerance to environmental stresses. Jatropha and Camelina, non-food oilseed crops, have also gained attention as potential biofuel feedstocks. These crops can be grown on marginal land, minimizing competition with food crops. Genetic engineering techniques have been explored to enhance their characteristics for biofuel production, including increasing oil yield, altering fatty acid profiles, and improving drought and environmental tolerance. The recent breakthrough in applying CRISPR/Cas (clustered regularly interspaced short palindromic repeat/CRISPR-associated) technology to manipulate the genomes of crops holds great promise, opening

up a realm of potential for targeted genetic modifications in bioenergy crops and various other species (Zhou et al. 2015). In addition to the examples provided earlier various genetically engineered energy crops that have been developed to enhance biofuel production, along with their specific target- genes are listed in Table 1.

Molecular Breeding

Molecular breeding techniques have emerged as valuable tools in enhancing the productivity, adaptability, and sustainability of bioenergy crops for biofuel production. These techniques, which include marker-based selection, genomic selection, and genetic modification, offer an efficient means for breeders to identify and select energy crop genotypes with desired traits. This expedites the development of superior varieties for bioenergy production. The specific traits targeted through these biotechnological approaches depend on the breeding priorities for each species but commonly encompass disease resistance, maximum yield potential, improved nutritional quality, waste reduction, and resistance to challenging climate conditions such as drought, heat, extreme cold and salt stress (Allwright and Taylor 2016). By utilizing these breeding approaches, it becomes possible to increase bioenergy crop yields without negatively impacting the environment necessitating additional land cultivation (Godfray et al. 2010). Consequently, the primary goal of bioenergy breeding is to achieve a sustainable intensification of yield, which involves increasing biomass production per unit of land area without causing environmental degradation or requiring increased agronomic inputs (Allwright and Taylor 2016). It is evident that advanced techniques such as next-generation sequencing (NGS), high-throughput genotyping, and molecular breeding play crucial roles in advancing the development of energy crops, similar to their contributions to agriculture. These tools offer immense potential for the improvement and optimization of bioenergy crops, leading to more efficient and sustainable biofuel production systems.

QTL analyses and genome-wide association studies (GWAS)

QTL mapping is a commonly used technique to identify specific genes associated with various traits of interest, typically by analyzing the linkage of markers to the trait. This method has been successfully applied to Arabidopsis, rice, maize, barley, and wheat, leading to the isolation of numerous genes. However, in sorghum, GWAS has gained popularity due to advancements in sequencing technology and its increased affordability. GWAS compares genetic variation among multiple lines, specifically single nucleotide polymorphisms (SNPs). Unlike QTL

Table 1 Examples of various genetically engineered energy crops which have been developed to enhance bioenergy production, along with their specific modified target- genes

Energy crop	Target genes	Function	References
Maize	<i>ZmMYB31</i>	Increased lignin content for improved biofuel production	Shen et al. (2013)
	<i>ZmMYB42</i>	Reduced lignin and cellulose content for improved bioethanol production	Fu et al. (2011)
	<i>ZmNAC111</i>	Enhanced drought tolerance and biomass production	Ding et al. (2023)
	<i>ZmPEPC</i>	Improved photosynthesis efficiency for increased biomass	Peng et al. (2018)
Poplar	<i>PtrMYB182</i>	Reduced lignin content for improved biofuel production	Voelker et al. (2010)
	<i>PtrMYB221</i>	Altered lignin composition for improved saccharification	Wang et al. (2021)
	<i>PtrMYB28</i>	Enhanced biomass production and reduced recalcitrance	Wang et al. (2016)
	<i>PtrGAUT12.1</i>	Increased xylan content and reduced recalcitrance	Biswal et al. (2015)
Rice	<i>OsMYB4</i>	Reduced lignin content for improved bioethanol production	Zhou et al. (2013)
	<i>OsNAC5</i>	Enhanced drought tolerance and biomass production	Jeong et al. (2010)
	<i>OsPPDK</i>	Improved photosynthesis efficiency for increased biomass	Zhao et al. (2012)
Jatropha	<i>MePIP1</i>	Improved water use efficiency and drought tolerance	Zou and Yang (2019)
	<i>MeCAX1</i>	Enhanced salt tolerance for cultivation in saline areas	Suo et al. (2012)
	<i>MeDREB2A</i>	Increased drought and heat tolerance	Tian et al. (2011)
Switchgrass	<i>PvMYB4</i>	Reduced lignin content for improved biofuel production	Baxter et al. (2015)
	<i>PvMYB40</i>	Altered lignin composition for improved saccharification	Shen et al. (2012a, b)
	<i>PvMYB60</i>	Enhanced biomass production and reduced recalcitrance	Vanholme et al. (2012)
	<i>PvCOMT</i>	Modified lignin biosynthesis pathway for improved biofuel production	Fu et al. (2011)
Sugarcane	<i>ScMYB4</i>	Reduced lignin content for improved bioethanol production	Tschaplinski et al. (2012)
	<i>ScDIR</i>	Enhanced drought tolerance and biomass production	Li et al. (2022a, b)
	<i>ScPPDK</i>	Improved photosynthesis efficiency for increased biomass	Peng et al. (2018)
	<i>ScSUS</i>	Enhanced sucrose accumulation for increased bioethanol production	Zhang et al. (2015)
Camelina	<i>BnWRI1</i>	Enhanced oil content and seed yield for biodiesel production	Zhao et al. (2012)
	<i>BnFAD2</i>	Increased oleic acid content for improved biodiesel quality	Nguyen et al. (2015)
	<i>BnDGAT1</i>	Enhanced triacylglycerol synthesis for increased oil yield	Liu et al. (2012)
algae	<i>ACCase</i>	Increased lipid production for biofuel production	Radakovits et al. (2012)
	<i>DGAT</i>	Enhanced triacylglycerol synthesis for increased oil yield	Pan et al. (2023)
Sorghum	<i>SbMyb60</i>	Increased lignin content and biomass yield	Scully et al. (2018)
Miscanthus	<i>ZmMYB31</i>	Enhanced biomass yield and reduced recalcitrance	Li et al. (2019)
Willow	<i>CCR</i>	Increase lignin digestibility	pan et al. (2014)
	<i>CAD</i>	reduce lignin content	Chen and Dixon (2007)
	<i>F5H</i>	Alters lignin composition	Vanholme et al. (2012)
Soybean	<i>FATB</i>	Increase oil content	Sun et al. (2014)
	<i>DGAT</i>	Enhances triacylglycerol	Roesler et al. (2016)
	<i>SAD</i>	Altered fatty acid composition	Zhang et al. (2015)
Eucalyptus	<i>4CL</i>	Alters lignin compositions	Fu et al. (2011)
	<i>CCOAOMT</i>	Modifies lignin structure	Li et al. (2003)
	<i>CAD</i>	Reduces lignin contents	Pilate et al. (2002)

analysis, which involves only two parental lines, GWAS involves a larger number of lines, detecting more QTLs but potentially lowering mapping accuracy. QTL analysis benefits from the ability to generate F2 populations consisting of hundreds of plants for precise genetic analysis and accurate mapping of the region of interest. On the other hand, GWAS relies on the length of linkage disequilibrium (LD) in the plant population, which determines

the genetic resolution of the target region. Therefore, the recommended approach is to initially employ GWAS to identify suitable lines and subsequently perform QTL analysis to refine the genetic mapping. For instance, Zou et al. (2012) constructed an ultra-high-density linkage map in sorghum using low-coverage sequences and SNPs derived from a recombinant inbred line (RIL) population. Following QTL analysis, they identified 57 major QTLs

associated with eight agronomically important traits, including heading date, plant height, node number, stem diameter, panicle neck length, and flag leaf width, under two photoperiod conditions. In another study, Morris et al. (2013) conducted GWAS on plant height components and inflorescence architecture using data from 336 lines in the sorghum association panel. Their GWAS analysis revealed several classical loci (*Dw1–Dw3*) related to plant height and candidate genes associated with inflorescence architecture. Similarly, Murray et al. (2009) conducted association mapping in sorghum using a panel of 125 genotypes, 47 simple sequence repeats (SSRs), and 322 SNP markers. They identified three significant associations for height.

Furthermore, the utilization of genotyping-by-sequencing (GBS) and transcriptome resequencing techniques in black cottonwood (*Populus trichocarpa*) has resulted in the identification of over 500,000 single nucleotide polymorphisms (SNPs) (Slavov et al. 2014; Gerald et al. 2013). This discovery has paved the way for the development of a 34,000 SNP genotyping array specifically designed for *P. trichocarpa*, encompassing more than 3500 genes (Gerald et al. 2013). The availability of this genotyping array has greatly facilitated numerous genome-wide association studies (GWAS) conducted in the past couple of years. Notably, comprehensive whole-genome resequencing investigations have revealed that linkage disequilibrium (LD) decay in poplar is extensive, enabling feasible association genetics studies with fewer markers than previously anticipated (Slavov et al. 2014). Recent research papers by Porth (2013) and McKown et al. (2014) have documented hundreds of trait-marker associations in *P. trichocarpa*, including economically important traits prioritized for bioenergy breeding. These traits encompass wood chemistry characteristics such as lignin content and composition, which have significant implications for feedstock processing and conversion to biofuels, as well as biomass yield and water use efficiency. Moreover, the genotyping array has been successfully employed to identify markers linked to rust severity in *P. trichocarpa*, a critical fungal infection that causes reduced biomass yields and economic losses (La Mantia et al. 2013). In the case of Miscanthus, more than 100,000 SNPs have been recently utilized in a GWAS to identify associations with phenology, cell wall composition, and biomass traits (Slavov et al. 2014). While poplar has established itself as a model tree species with significant sequencing efforts, leading to the identification of SNPs and trait-marker associations, Miscanthus has made more recent progress with the establishment of association mapping populations and the publication of an extensive GBS and GWAS study (Slavov et al. 2014). Switchgrass has undergone substantial resequencing and

genotyping efforts, although GWAS studies have not been conducted thus far. Willow lags behind the other feedstocks, as no GBS or GWAS studies have been published to date.

Genome-wide association Studies (GWAS) have identified trait marker associations that can be utilized for Marker-Assisted Selection (MAS). This advancement enables the early identification of highly valuable individuals in a population, resulting in improved selection efficiency and reduced selection time (Miedaner and Korzun 2012). With the availability of increasingly extensive marker sets, the adoption of whole-genome MAS approaches is now becoming feasible (Xu et al. 2012). Furthermore, the continuous progress in marker density is expected to facilitate the implementation of Genomic Selection (GS) in plant species, a technique already widely utilized in animal breeding (Ashraf et al. 2013). GS involves phenotyping a large training population and determining breeding values based solely on genotyped markers associated with the desired traits (Tester and Langridge 2010). Computational studies suggest that the integration of GS in forest tree breeding has the potential to significantly enhance selection efficiency and reduce the breeding cycle (Ashraf et al. 2013). This is particularly encouraging for bioenergy, poplar, and willow, as conventional breeding methods for these species are time-consuming and require substantial space to maintain a reproductively mature population. Additionally, Miscanthus displays notable phenotypic and genetic variation, indicating that the implementation of GS in Miscanthus breeding programs is now viable following the successful utilization of Genotyping-by-Sequencing (GBS) and GWAS techniques (Slavov et al. 2014).

Classical linkage analysis will also continue to play a vital role in the identification of Quantitative Trait Loci (QTL) that impact complex biomass accumulation and cell wall architecture traits. In a study conducted by Andre et al. (2010), the authors investigated 223 recombinant inbred lines derived from the IBM population (Lee et al. 2002). These lines were carefully examined for variations in biomass characteristics, including conversion efficiency after dilute acid pretreatment. Despite the limited range of variation observed within the population (e.g., lignin content on a cell wall basis ranged from 20.3% to 21.9% across the experimental panel), the researchers successfully discovered 152 QTLs with small effects that were associated with various traits related to cell wall composition and cellulosic ethanol production. It is crucial to complement the knowledge gained from linkage studies with insights from numerous previous studies on forage maize, which have already identified significant QTLs related to cell wall digestibility, lignin content, and lignin composition. The advent of high-throughput

genotyping platforms that focus on single nucleotide polymorphisms, advanced statistical models, and high-resolution mapping panels (such as the Nested Association Mapping Panel of maize) is anticipated to expedite genome-wide association studies targeting both biomass yield and quality characteristics (Riedelsheimer et al. 2012; Windhausen et al. 2012; Wallace et al. 2014).

Genetic modification for bioenergy crops

Another alternative approach to improve traits is offered by genetic modification (GM), which has garnered significant attention and generated both benefits and controversy about food and bioenergy crops. The potential of GM technology for bioenergy production has also been explored in studies focusing on grasses (Jakob et al. 2011) and woody crops (Hinchee et al. 2011). However, a significant challenge in achieving cost-effective and sustainable second-generation feedstocks is lignin recalcitrance. This barrier necessitates energy-intensive and potentially expensive thermochemical pretreatment before the saccharification of polysaccharides to obtain simple sugars for fermentation (Gomez et al. 2008). Consequently, understanding the genetic mechanisms behind lignin biosynthesis and the regulation of lignin content and composition has become a crucial research priority. Extensive efforts have been devoted to developing low-lignin transgenic plants, employing techniques such as knockout mutations or RNA silencing, both in model organisms like *Arabidopsis thaliana* and in other bioenergy crops (Etchells et al. 2015). Significant progress has been made in altering or suppressing lignin biosynthesis in transgenic poplar, resulting in reduced recalcitrance, increased ethanol yield, and improved conversion efficiency. However, it is important to note that these modifications often come at the cost of compromised fitness and reduced yield when implemented in field conditions.

There have been concerns raised regarding the potential vulnerability of low-lignin transgenic plants to pests and infections, particularly rust, a common pathogen affecting poplar trees (Polle et al. 2013). However, there is currently no supporting evidence to validate this claim. Poplar trees have a natural defence mechanism against rust infection, which involves upregulating genes associated with the phenylpropanoid pathway and accumulating monolignols (Miranda et al. 2007). However, manipulating these genes through genetic modifications in bioenergy poplar plantations could inadvertently heighten susceptibility to rust infection (Polle et al. 2013). To address this concern, a promising alternative approach has emerged, focusing on modifying the lignin structure instead of reducing its content (Wilkinson et al. 2014). This approach entails introducing a

genetically modified enzyme called *monolignol ferulate transferase*, which incorporates ester linkages into the lignin polymer backbone. Consequently, the modified lignin becomes more easily broken down using a milder pretreatment protocol. Crucially, transgenic poplar trees expressing this enzyme did not exhibit any reduction in lignin content or phenotypic abnormalities under controlled greenhouse conditions. By reducing the severity of the required pretreatment, this strategy is expected to significantly enhance the cost-effectiveness and sustainability of producing lignocellulosic bioethanol. The successful targeting of the lignin biosynthetic pathway has also been demonstrated in transgenic switchgrass, leading to improved ethanol yields. A promising two-year field trial of low-lignin transgenic switchgrass showed increased sugar release and ethanol production, without any adverse effects on biomass yield or heightened susceptibility to rust in this energy grass species (Baxter et al. 2015).

Apart from the pathway involved in lignin production, the introduction of pine glutamine synthetase (*GS1a*) into poplar trees has exhibited remarkable improvements in the composition of wood and increased solubility of lignin, without compromising the yield (Coleman et al. 2012). These genetically modified trees displayed higher levels of S-lignin and elevated concentrations of wood sugars like glucose, galactose, mannose, and xylose. These results indicate that overexpressing *GS1a* could be a promising strategy for the development of biofuels. Additionally, *GS1a* plays a vital role in nitrogen metabolism, leading to enhanced nitrogen assimilation efficiency and improved growth (Man et al. 2005). It has also been associated with enhanced drought tolerance (el-Khatib et al. 2004). In terms of drought resistance, the overexpression of *GS1a* resulted in increased expression of photosynthetic enzymes and higher chlorophyll content in transgenic lines. These effects aided in maintaining the electron transport capacity during water scarcity. Another approach to promote growth in transgenic poplar involves the expression of *Arabidopsis* nucleoside diphosphate kinase 2 (*NDPK2*), which regulates the expression of antioxidant genes and potentially enhances tolerance to oxidative stress (Kim et al. 2011). Similarly, transgenic switchgrass has been engineered to exhibit enhanced growth through the overexpression of a regulatory microRNA involved in apical dominance (Fu et al. 2012). These growth-enhancing modifications could be particularly useful for cultivating second-generation biofuels on marginal or degraded lands, minimizing competition for agricultural resources. Such bioenergy plantations have the potential to provide low-carbon energy while aiding in land reclamation and phytoremediation efforts, thereby offering local environmental

benefits. Furthermore, studies have shown that poplar trees genetically modified to contain the yeast cadmium factor 1 (*ScYCF1*) gene exhibit enhanced growth and possess the capacity to effectively accumulate heavy metals in soils contaminated by mining waste (Shim et al. 2013). Addressing salinity, a significant challenge impacting soil quality and agriculture, transgenic poplar with increased superoxide dismutase (SOD) activity exhibited enhanced salt tolerance and substantial growth improvement in saline soil (Wang et al. 2010). Recently, the successful application of CRISPR/Cas technology in poplar and other bioenergy crops has opened up new possibilities for precise genome editing (Zhou et al. 2015). This advancement allows for targeted modifications and holds great potential for further advancements in enhancing bioenergy crops.

Biorefinery processes

Biotechnological advancements can also contribute to the development of more efficient and cost-effective biorefinery processes for converting plant biomass into biofuels and other valuable products. These processes involve various steps, such as enzymatic hydrolysis, fermentation, and other conversion technologies. Lignocellulosic biomass, derived from non-edible sources like woody biomass, crop residues, energy crops, municipal wastes, and algae, shows potential promise as a feedstock for biorefineries. Unlike traditional biofuel feedstocks like corn or sugarcane, these Next-generation feedstocks have the advantage of not conflicting with food production and can often be cultivated on unproductive or underutilized agricultural land (Ragauskas et al. 2006).

The chemical steps involved in creating biofuels from lignocellulose typically include biomass collection, polymer breakdown into sugars, and sugar conversion into ethanol or other biofuels. Common methods to extract energy from lignocellulosic biomass involve utilizing heat and/or acid treatments to separate lignin from cellulose and hemicellulose. Enzymatic hydrolysis, fermentation, and distillation are frequently employed techniques in this process. However, a key hurdle in effectively utilizing lignocellulosic biomass in biorefinery is its inherent resistance to breakdown, known as recalcitrance. This recalcitrance stems from factors such as the intricate structure of the biomass, the interactions between lignin and hemicellulose, and the robust hydrogen bonding within crystalline cellulose. Overcoming recalcitrance necessitates the study of plant cell wall biosynthesis, exploration of various pretreatment methods, and the development of efficient enzymatic hydrolysis techniques. These approaches aim to disintegrate the complex carbohydrates in plant biomass into fermentable

sugars for economically viable ethanol production (Kristensen et al. 2008; Louime et al. 2012).

Genomics plays a crucial role in driving the advancement of eco-friendly bioenergy sources and conversion methods. Through the examination of the genetic composition and characteristics of organisms involved in biofuel production, scientists can enhance and refine natural processes that have evolved over extended periods. This encompasses genetic investigation and manipulation of renewable fuel sources, as well as the microorganisms and enzymes responsible for transforming these fuel sources into usable energy. By leveraging the potential of genomics, researchers strive to address the escalating energy demands of society while prioritizing environmental sustainability. These represent only a handful of avenues in which genomics is influencing the advancement of renewable bioenergy sources and conversion techniques, with numerous untapped genetic solutions waiting for exploration. In the forthcoming years, scientists will continue to seek inspiration from nature to combat the global energy crisis. By employing genomic research and engineering techniques to optimize renewable fuel sources and the microorganisms and enzymes involved in their conversion, we have remarkable opportunities to tap into billions of years of evolutionary advancements and leverage them towards addressing our growing energy demands in a sustainable and environmentally responsible manner.

Concluding remarks

Bioenergy development offers a significant opportunity to address greenhouse gas emissions and achieve energy independence from fossil fuels by utilizing biomass for power generation. When crop biomass is used as an energy source, the carbon dioxide (CO₂) released during combustion is absorbed by plants during their growth, resulting in no net increase in CO₂ levels. This renewable energy alternative has the potential to diversify agricultural production systems. In the field of bioenergy crops, substantial advancements have been made through the application of genetic engineering and molecular breeding techniques. These techniques, including QTL mapping and genetic modification, show promise in enhancing the productivity and stress tolerance of bioenergy crops. Moreover, they enable the identification of markers and candidate genes related to crucial bioenergy traits such as growth, disease resistance, and feedstock quality. While traditional breeding programs have already made notable progress in bioenergy crop improvement, the emergence of molecular biotechnology has opened up new possibilities for marker-assisted breeding and genetic engineering. Genomic strategies for selection and breeding have

become a reality and are expected to propel future breeding programs. The integration of advanced molecular techniques, whether through genomic deployment or other approaches, will be vital for the development of high-yielding and sustainable non-food bioenergy crops. The successful implementation of these advanced molecular techniques is of utmost significance as nations worldwide strive to fulfil their renewable energy commitments. By harnessing the power of genetic engineering and molecular breeding, researchers and breeders can work towards the sustainable intensification of non-food bioenergy crops. These crops can be cultivated in marginal agricultural lands and challenging climatic conditions, thus contributing to the diversification of energy sources and the reduction of greenhouse gas emissions. In conclusion, the application of advanced molecular techniques, such as genetic engineering and marker-assisted breeding, will play a central role in the advancement of high-yielding, sustainable biofuel crops. These crops hold the promise potential to meet renewable energy demands while minimizing environmental impacts, thereby supporting global initiatives to transition towards a more sustainable energy future.

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Author's contribution

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References

Abramson M, Shoseyov O, Shani Z. Plant cell wall reconstruction toward improved lignocellulosic production and processability. *Plant Sci.* 2010;178:61–72. <https://doi.org/10.1016/j.plantsci.2009.11.003>.

- Agostini F, Gregory AS, Richter GM. Carbon sequestration by perennial energy crops: is the jury still out? *Bioenergy Research.* 2015;8(3):1057–80. <https://doi.org/10.1007/s12155-014-9571-0>.
- Ale, S., Femeena, P.V., Mehan, S. and Cibin, R., 2019. Environmental impacts of bioenergy crop production and benefits of multifunctional bioenergy systems. In *Bioenergy with carbon capture and storage* (pp. 195–217). Academic Press. <https://doi.org/10.1016/B978-0-12-816229-3.00010-7>
- Allwright MR, Taylor G. Molecular breeding for improved second-generation bioenergy crops. *Trends Plant Sci.* 2016;21(1):43–54. <https://doi.org/10.1016/j.tplants.2015.10.002>.
- Anders N, Wilkinson MD, Lovegrove A, Freeman J, Tryfona T, Pellny TK, Weimar T, Mortimer JC, Stott K, Baker JM, Defoin-Platel M. Glycosyl transferases in family 61 mediate *arabinofuranosyl transfer* onto xylan in grasses. *Proc Natl Acad Sci.* 2012;109(3):989–93. <https://doi.org/10.1073/pnas.1115858109>.
- Andre A, Diamantopoulou P, Philippoussis A, Sarris D, Komaitis M, Papanikolaou S. Biotechnological conversions of bio-diesel derived waste glycerol into added-value compounds by higher fungi: production of biomass, single cell oil and oxalic acid. *Ind Crops and Prod.* 2010;31(2):407–16. <https://doi.org/10.1016/j.indcrop.2009.12.011>.
- Ashraf M, Foolad MR. Crop breeding for salt tolerance in the era of molecular markers and marker-assisted selection. *Plant Breed.* 2013;132:10–20. <https://doi.org/10.1111/pbr.12000>.
- Baenziger PS, Russell WK, Graef GL, Campbell BT. Improving lives: 50 years of crop breeding, genetics, and cytology (C-1). *Crop Sci.* 2006;46(5):2230–44. <https://doi.org/10.2135/cropsci2005.11.0404gas>.
- Barriere Y, Ralph J, Mechin V, Guillaumie S, Grabber JH, Argillier O, Chabbert B, Lapiere C. Genetic and molecular basis of grass cell wall biosynthesis and degradability. II. Lessons from brown-midrib mutants. *Crit Rev Biol.* 2004;327:847–60. <https://doi.org/10.1016/j.crv.2004.05.010>.
- Baxter HL, Poovaiah CR, Yee KL, Mazarei M, Rodriguez M, Thompson OA, Shen H, Turner GB, Decker SR, Sykes RW, Chen F. Field evaluation of transgenic switchgrass plants overexpressing PvMYB4 for reduced biomass recalcitrance. *BioEnergy Research.* 2015;8:910–21. <https://doi.org/10.1007/s12155-014-9570-1>.
- Belyakov, N., 2019. Sustainable Power Generation. Current status, Future challenges, and perspectives, pp.417–438. <https://doi.org/10.1016/B978-0-12-817012-0.00031-1>
- Biswal AK, Hao Z, Pattathil S, Yang X, Winkeler K, Collins C, Mohanty SS, Richardson EA, Gelineo-Albersheim I, Hunt K, Ryno D. Downregulation of GAUT2 in *Populus deltoides* by RNA silencing results in reduced recalcitrance, increased growth and reduced xylan and pectin in a woody biofuel feedstock. *Biotechnol Biofuels.* 2015;8(1):1–26. <https://doi.org/10.1186/s13068-015-0218-y>.
- Chapotin SM, Wolt JD. Genetically modified crops for the bioeconomy: meeting public and regulatory expectations. *Transgen Res.* 2007;16:675–88. <https://doi.org/10.1007/s11248-007-9122-y>.
- Chen F, Dixon RA. Lignin modification improves fermentable sugar yields for biofuel production. *Nat Biotechnol.* 2007;25(7):759–61. <https://doi.org/10.1038/nbt1316>.
- Coleman HD, Cánovas FM, Man H, Kirby EG, Mansfield SD. Enhanced expression of glutamine synthetase (GS1a) confers altered fiber and wood chemistry in field grown hybrid poplar (*Populus tremula alba*) (717–1B4). *Plant Biotechnol J.* 2012;10:883–9. <https://doi.org/10.1111/j.1467-7652.2012.00714.x>.
- Collard BC, Mackill DJ. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philos Trans R Soc B.* 2008;363:557–72. <https://doi.org/10.1098/rstb.2007.2170>.
- Correa DF, Beyer HL, Fargione JE, Hill JD, Possingham HP, Thomas-Hall SR, Schenk PM. Towards the implementation of sustainable biofuel production systems. *Renew Sustain Energy Rev.* 2019;107:250–63. <https://doi.org/10.1016/j.rser.2019.03.005>.
- Daley J. The EPA declared that burning wood is carbon neutral. It's actually a lot more complicated. *Smithsonian magazine*; 2018.
- de Leon N, Coors JG. Genetic improvement of corn for lignocellulosic feedstock production. In: Vermerris W, editor. *Genetic Improvement of Bioenergy Crops*. New York: Springer; 2008. p. 185–210.
- de Siqueira Ferreira S, Nishiyama MY, Paterson AH, Souza GM. Biofuel and energy crops: high-yield Saccharinae take centre stage in the post-genomics era. *Genome Biol.* 2013;14:1–12. <https://doi.org/10.1186/gb-2013-14-6-210>.

- Ding N, Zhao Y, Wang W, Liu X, Shi W, Zhang D, Chen J, Ma S, Sun Q, Wang T, Lu M. Transcriptome analysis in contrasting maize inbred lines and functional analysis of five maize NAC genes under drought stress treatment. *Front Plant Sci.* 2023;13:1097719. <https://doi.org/10.3389/fpls.2022.1097719>.
- El-Khatib RT, Hamerlynck EP, Gallardo F, Kirby EG. Transgenic poplar characterized by ectopic expression of a pine cytosolic glutamine synthetase gene exhibits enhanced tolerance to water stress. *Tree Physiol.* 2004;24:729–36. <https://doi.org/10.1093/treephys/24.7.729>.
- Etchells JP, Mishra LS, Kumar M, Campbell L, Turner SR. Wood formation in trees is increased by manipulating PXY-regulated cell division. *Curr Biol.* 2015;25:1050–5. <https://doi.org/10.1016/j.cub.2015.02.023>.
- Fischer G, Prieler S, van Velthuisen HT, Lensink SM, Londo M, de Wit M. Biofuel production potentials in Europe: Sustainable use of cultivated land and pastures. Part I: Land productivity potentials. *Biomass Bioenerg.* 2010;34:159–72. <https://doi.org/10.1016/j.biombioe.2009.07.008>.
- Fu C, Xiao X, Xi Y, Ge Y, Chen F, Bouton J, Dixon RA, Wang ZY. Downregulation of cinnamyl alcohol dehydrogenase (CAD) leads to improved saccharification efficiency in switchgrass. *BioEnergy Research.* 2011;4(3):153–64. <https://doi.org/10.1007/s12155-010-9109-z>.
- Fu C, Sunkar R, Zhou C, Shen H, Zhang JY, Matts J, Wolf J, Mann DG, Stewart-Tang CNY, Wang ZY. Overexpression of miR156 in switchgrass (*Panicum virgatum* L.) results in various morphological alterations and leads to improved biomass production. *Plant Biotechnol J.* 2012;10:443–52. <https://doi.org/10.1111/j.1467-7652.2011.00677.x>.
- George, E. F., 2008. Plant tissue culture procedure background. In E. F. George, M. A. Hall, & G.-J. De Klerk (Eds.), *Plant propagation by tissue culture* (pp. 1–29). Dordrecht: Springer. https://doi.org/10.1007/978-1-4020-5005-3_1
- Geraldes A, Difazio SP, Slavov GT, Ranjan P, Muchero W, Hannemann J, Gunter LE, Wymore AM, Grassa CJ, Farzaneh N, Porth I. A 34K SNP genotyping array for *Populus trichocarpa*: design, application to the study of natural populations and transferability to other *Populus* species. *Mol Ecol Resour.* 2013;13:306–23. <https://doi.org/10.1111/1755-0998.12056>.
- Gielen D, Boshell F, Saygin D, Bazilian MD, Wagner N, Gorini R. The role of renewable energy in the global energy transformation. *Energy Strat Rev.* 2019;24:38–50. <https://doi.org/10.1016/j.esr.2019.01.006>.
- Godfray H CJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C. Food security: the challenge of feeding 9 billion people. *Science.* 2010;327:812–8. <https://doi.org/10.1126/science.1185383>.
- Gomez LD, Steele-King CG, McQueen-Mason SJ. Sustainable liquid biofuels from biomass: the writing's on the walls. *New Phytol.* 2008;178:473–85. <https://doi.org/10.1111/j.1469-8137.2008.02422.x>.
- Gressel J. Transgenics are imperative for biofuel crops. *Plant Sci.* 2008;174(3):246–63. <https://doi.org/10.1016/j.plantsci.2007.11.009>.
- Gresshoff PM, Rangan L, Indrasumunar A, Scott PT. A new bioenergy crop based on oil-rich seeds from the legume tree *Pongamia pinnata*. *Energy Emission Control Technol.* 2017;5:19–26. <https://doi.org/10.2147/EECT.S69854>.
- Harfouche A, Meilan R, Altman A. Tree genetic engineering and applications to sustainable forestry and biomass production. *Trends Biotechnol.* 2011;29(1):9–17. <https://doi.org/10.1016/j.tibtech.2010.09.003>.
- Heaton EA, Flavell RB, Mascia PN, Thomas SR, Dohleman FG, Long SP. Herbaceous energy crop development: Recent progress and future prospects. *Curr Opin Biotechnol.* 2008;19:202–9. <https://doi.org/10.1016/j.copbio.2008.05.001>.
- Hinchee M, Rottmann W, Mullinax L, Zhang C, Chang S, Cunningham M, Pearson L, Nehra N. Short-rotation woody crops for bioenergy and biofuel applications. *In Vitro Cell Dev Biol Plant.* 2011;45:619–29. <https://doi.org/10.1007/s11627-009-9235-5>.
- Jakob K, Zhou F, Paterson AH. Genetic improvement of C4 grasses as cellulosic biofuel feedstocks. *In Vitro Cell Dev Biol Plant.* 2011;45:291–305. <https://doi.org/10.1007/s11627-009-9214-x>.
- Jansson S, Douglas CJ. *Populus*: a model system for plant biology. *Annu Rev Plant Biol.* 2007;58(435–458):23. <https://doi.org/10.1146/annurev.arplant.58.032806.103956>.
- Jeong JS, Kim YS, Baek KH, Jung H, Ha SH, Do Choi Y, Kim M, Reuzeau C, Kim JK. Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under field drought conditions. *Plant Physiol.* 2010;153(1):185–97. <https://doi.org/10.1104/pp.110.154773>.
- Jeswani HK, Chilvers A, Azapagic A. Environmental sustainability of biofuels: a review. *Proceedings of the Royal Society a.* 2020;476(2243):20200351. <https://doi.org/10.1098/rspa.2020.0351>.
- Jorge M. The use of bioenergy for electricity generation, in (Ed) *Non-Conventional Energy in North America*; 2022, p. 261–326. <https://doi.org/10.1016/B978-0-12-823440-2.00008-1>
- Karp A, Shield I. Bioenergy from plants and the sustainable yield challenge. *New Phytol.* 2008;179(1):15–32. <https://doi.org/10.1111/j.1469-8137.2008.02432.x>.
- Khodakovskaya MV, de Silva K, Nedosekin DA, Dervishi E, Biris AS, Shashkov EV, Galanzha EI, Zharov VP. Complex genetic, photothermal, and photoacoustic analysis of nanoparticle-plant interactions. *Proc Natl Acad Sci.* 2011;108(3):1028–33. <https://doi.org/10.1073/pnas.1008856108>.
- Kim YH, Kim MD, Choi YI, Park SC, Yun DJ, Noh EW, Lee HS, Kwak SS. Transgenic poplar expressing Arabidopsis NDPK2 enhances growth as well as oxidative stress tolerance. *Plant Biotechnol J.* 2011;9:334–47. <https://doi.org/10.1111/j.1467-7652.2010.00551.x>.
- Kristensen E, Bouillon S, Dittmar T, Marchand C. Organic carbon dynamics in mangrove ecosystems: a review. *Aquat Bot.* 2008;89(2):201–19. <https://doi.org/10.1016/j.aquabot.2007.12.005>.
- La Mantia J, Klápště J, El-Kassaby YA, Azam S, Guy RD, Douglas CJ, Mansfield SD, Hamelin R. Association analysis identifies *Melampsora columbiana* poplar leaf rust resistance SNPs. *PLoS ONE.* 2013;8:e78423. <https://doi.org/10.1371/journal.pone.0078423>.
- Lakshmanan P, Geiskes RJ, Aitken KS, Grof CLP, Bonnett GD, Smith GR. Sugarcane biotechnology: The challenges and opportunities. *In Vitro Cell Dev Biol-Plant.* 2005;41:345–61. <https://doi.org/10.1079/IVP2005643>.
- Lee M, Sharopova N, Beavis WD, Grant D, Katt M, Blair D, Hallauer A. Expanding the genetic map of maize with the intermated B73x Mo17 (IBM) population. *Plant Mol Biol.* 2002;48:453–61. <https://doi.org/10.1023/A:1014893521186>.
- Li L, Zhou Y, Cheng X, Sun J, Marita JM, Ralph J, Chiang VL. Combinatorial modification of multiple lignin traits in trees through multigene cotransformation. *Proc Natl Acad Sci.* 2003;100(8):4939–44. <https://doi.org/10.1073/pnas.0831166100>.
- Li M, Lin L, Zhang Y, Sui N. ZmMYB31, a R2R3-MYB transcription factor in maize, positively regulates the expression of CBF genes and enhances resistance to chilling and oxidative stress. *Mol Biol Rep.* 2019;46:3937–44. <https://doi.org/10.1007/s11033-019-04840-5>.
- Li W, Wang L, Qi Y, Xie Y, Zhao W, Dang Z, Zhang J. Overexpression of WRINKLED1 improves the weight and oil content in seeds of flax (*Linum usitatissimum* L.). *Front Plant Sci.* 2022;13:1003758. <https://doi.org/10.3389/fpls.2022.1003758>.
- Li X, Liu Z, Zhao H, Deng X, Su Y, Li R, Chen B. Overexpression of sugarcane ScDIR genes enhances drought tolerance in *Nicotiana benthamiana*. *Int J Mol Sci.* 2022b;23(10):5340. <https://doi.org/10.3390/ijms23105340>.
- Lin S, Reppert J, Hu Q, Hudson JS, Reid ML, Ratnikova TA, Rao AM, Luo H, Ke PC. Uptake, translocation, and transmission of carbon nanomaterials in rice plants. *Small.* 2009;5(10):1128–32. <https://doi.org/10.1002/sml.200801556>.
- Liu J, Wu J, Liu F, Han X. Quantitative assessment of bioenergy from crop stalk resources in Inner Mongolia. *China. Appl Energy.* 2012;93:305–18. <https://doi.org/10.1016/j.apenergy.2011.12.059>.
- Loume C, Marshall RW, Vasanthaiah HK, Onokpise O. Genomics and potential bioenergy applications in the developing world. *Genomics Applications for the Developing World*; 2012, pp.263–272. https://doi.org/10.1007/978-1-4614-2182-5_15
- Lu Y, Mosier NS. Current technologies for fuel ethanol production from lignocellulosic plant biomass. In: Vermeris W (ed), *Genetic Improvement of Bioenergy Crops*, Springer, New York; 2008, pp 161–182. https://doi.org/10.1007/978-0-387-70805-8_6
- Lynd LR, Laser MS, Bransby D, Dale BE, Davison B, Hamilton R, Himmel M, Keller M, McMillan JD, Sheehan J, Wyman CE. How biotech can transform biofuels. *Nat Biotechnol.* 2008;26(2):169–72. <https://doi.org/10.1038/nbt0208-169>.
- Malode SJ, Prabhu KK, Mascarenhas RJ, Shetti NP, Aminabhavi TM. Recent advances and viability in biofuel production. *Energy Conv Manag.* 2021;10:100070. <https://doi.org/10.1016/j.ecmx.2020.100070>.
- Man HM, Boriel R, El-Khatib R, Kirby EG. Characterization of transgenic poplar with ectopic expression of pine cytosolic glutamine synthetase under

- conditions of varying nitrogen availability. *New Phytol.* 2005;167:31–9. <https://doi.org/10.1111/j.1469-8137.2005.01461.x>.
- Margaritopoulou T, Roka L, Alexopoulou E, Christou M, Rigas S, Haralampidis K, Milioni D. Biotechnology towards energy crops. *Mol Biotechnol.* 2016;58:149–58. <https://doi.org/10.1007/s12033-016-9913-6>.
- Massman JM, Jung HJG, Bernardo R. Genome-wide selection versus marker-assisted recurrent selection to improve grain yield and Stover-quality traits for cellulosic ethanol in maize. *Crop Sci.* 2013;53:58–66. <https://doi.org/10.2135/cropsci2012.02.0112>.
- McKown AD, Klápště J, Guy RD, Geraldes A, Porth I, Hannemann J, Friedmann M, Muchero W, Tuskan GA, Ehling J, Cronk QC. Genome-wide association implicates numerous genes underlying ecological trait variation in natural populations of *Populus trichocarpa*. *New Phytol.* 2014;203:535–53. <https://doi.org/10.1111/nph.12815>.
- McQualter RB, Dale JL, Harding RM, McMahon JA. Production and evaluation of transgenic sugarcane containing a Fiji disease virus (FDV) genome segment 59-derived synthetic resistance gene. *Aust J Agric Res.* 2004;55:139–45. <https://doi.org/10.1071/AR03131>.
- Miedaner T, Korzun V. Marker-assisted selection for disease resistance in wheat and barley breeding. *Phytopathology.* 2012;102:560–6. <https://doi.org/10.1094/PHYTO-05-11-0157>.
- Miranda M, Ralph SG, Mellway R, White R, Heath MC, Bohlmann J, Constabel CP. The transcriptional response of hybrid poplar (*Populus trichocarpa* P. deltoides) to infection by *Melampsora medusae* leaf rust involves induction of flavonoid pathway genes leading to the accumulation of proanthocyanidins. *Mol Plant Microbe Interact.* 2007;20:816–31. <https://doi.org/10.1094/MPMI-20-7-0816>.
- Mola-Yudego B, Aronsson P. Yield models for commercial willow biomass plantations in Sweden. *Biomass Bioenerg.* 2008;32(9):829–37. <https://doi.org/10.1016/j.biombioe.2008.01.002>.
- Morales Pedraza J. Chapter 4-Current Status and Perspective in the Use of Coal for Electricity Generation in the North American Region. *Conventional Energy in North America*, pp.211–257. Morales Pedraza, J., Ed.; Elsevier: Amsterdam, The Netherlands; 2019, pp. 211–257. <https://doi.org/10.1016/B978-0-12-814889-1.00004-8>
- Morris GP, Ramu P, Deshpande SP, Hash CT, Shah T, Upadhyaya HD, Riera Lizarazu O, Brown PJ, Acharya CB, Mitchell SE, Harriman J, Glaubitz JC, Buckler ES, Kresovich S. Population genomic and genome-wide association studies of agroclimatic traits in sorghum. *Proc Natl Acad Sci USA.* 2013;110:453–8. <https://doi.org/10.1073/pnas.1215985110>.
- Murray SC, Rooney WL, Hamblin MT, Mitchell SE, Kresovich S. Sweet sorghum genetic diversity and association mapping for brix and height. *Plant Genome.* 2009;2:48–62. <https://doi.org/10.3835/plantgenome2008.10.0011>.
- Nair LG, Agrawal K, Verma P. An overview of sustainable approaches for bioenergy production from agro-industrial wastes. *Energy Nexus.* 2022;6:100086. <https://doi.org/10.1016/j.nexus.2022.100086>.
- Nguyen HT, Park H, Koster KL, Cahoon RE, Nguyen HT, Shanklin J, Clemente TE, Cahoon EB. Redirection of metabolic flux for high levels of omega-7 monounsaturated fatty acid accumulation in camelina seeds. *Plant Biotechnol J.* 2015;13(1):38–50. <https://doi.org/10.1111/pbi.12233>.
- Pan H, Zhou R, Louie GV, Mühlemann JK, Bomati EK, Bowman ME, Dudareva N, Dixon RA, Noel JP, Wang X. Structural studies of cinnamoyl-CoA reductase and cinnamyl-alcohol dehydrogenase, key enzymes of monolignol biosynthesis. *Plant Cell.* 2014;26(9):3709–27. <https://doi.org/10.1105/tpc.114.127399>.
- Pan P, Xing Y, Zhang D, Wang J, Liu C, Wu D, Wang X. A review of the identification of transgenic oilseeds and oils. *J Food Sci.* 2023;88(80):3189–203. <https://doi.org/10.1111/1750-3841.16705>.
- Pandey K, Lahiani MH, Hicks VK, Hudson MK, Green MJ, Khodakovskaya M. Effects of carbon-based nanomaterials on seed germination, biomass accumulation and salt stress response of bioenergy crops. *PLoS ONE.* 2018;13(8):e0202274. <https://doi.org/10.1371/journal.pone.0202274>.
- Peng C, Xu W, Hu L, Li Y, Qi X, Wang H, Hua X, Zhao M. Effects of the maize C 4 phosphoenolpyruvate carboxylase (ZmPEPC) gene on nitrogen assimilation in transgenic wheat. *Plant Growth Regul.* 2018;84:191–205. <https://doi.org/10.1007/s10725-017-0332-x>.
- Pilate G, Guiney E, Holt K, Petit-Conil M, Lapierre C, Leplé JC, Pollet B, Mila I, Webster EA, Marstorp HG, Hopkins DW. Field and pulping performances of transgenic trees with altered lignification. *Nat Biotechnol.* 2002;20(6):607–12. <https://doi.org/10.1038/nbt0602-607>.
- Polle A, Janz D, Teichmann T, Lipka V. Poplar genetic engineering: promoting desirable wood characteristics and pest resistance. *Appl Microbiol Biotechnol.* 2013;97:5669–79. <https://doi.org/10.1007/s00253-013-4940-8>.
- Porth I, Klapšte J, Skyba O, Hannemann J, McKown AD, Guy RD, DiFazio SP, Muchero W, Ranjan P, Tuskan GA, Friedmann MC. Genome-wide association mapping for wood characteristics in *Populus* identifies an array of candidate single nucleotide polymorphisms. *New Phytol.* 2013;200:710–26. <https://doi.org/10.1111/nph.12422>.
- Radakovits R, Jinkerson RE, Fuerstenberg SI, Tae H, Settlage RE, Boore JL, Posewitz MC. Draft genome sequence and genetic transformation of the oleaginous alga *Nannochloropsis gaditana*. *Nat Commun.* 2012;3(1):686. <https://doi.org/10.1038/ncomms1688>.
- Ragauskas AJ, Williams CK, Davison BH, Britovsek G, Cairney J, Eckert CA, Frederick WJ Jr, Hallett JP, Leak DJ, Liotta CL, Mielenz JR. The path forward for biofuels and biomaterials. *Science.* 2006;311(5760):484–9. <https://doi.org/10.1126/science.114736>.
- Resende Jr MFR, Munoz P, Acosta JJ, Peter GF, Davis JM, Grattapaglia D, Resende MDV, Kirst M. Accelerating the domestication of trees using genomic selection: accuracy of prediction models across ages and environments. *New Phytol.* 2012;193:617–24. <https://doi.org/10.1111/j.1469-8137.2011.03895.x>.
- Riedelsheimer C, Czedik-Eysenberg A, Grieder C, Lisek J, Technow F, Sulpire R, Altmann T, Stitt M, Willmitzer L, Melchinger AE. Genomic and metabolic prediction of complex heterotic traits in hybrid maize. *Nat Genet.* 2012;44:217–20. <https://doi.org/10.1038/ng.1033>.
- Rodionova MV, Poudyal RS, Tiwari I, Voloshin RA, Zharmukhamedov SK, Nam HG, Zayadan BK, Bruce BD, Hou HJ, Allakhverdiev SI. Biofuel production: challenges and opportunities. *Int J Hydrogen Energy.* 2017;42(12):8450–61. <https://doi.org/10.1016/j.ijhydene.2016.11.125>.
- Roesler K, Shen B, Bermudez E, Li C, Hunt J, Damude HG, Ripp KG, Everard JD, Booth JR, Castaneda L, Feng L. An improved variant of soybean type 1 diacylglycerol acyltransferase increases the oil content and decreases the soluble carbohydrate content of soybeans. *Plant Physiol.* 2016;171(2):878–93. <https://doi.org/10.1104/pp.16.00315>.
- Saballos A. Development and utilization of sorghum as a bioenergy crop. In: Vermerris W (ed), *Genetic Improvement of Bioenergy Crops*. Springer, New York; 2008, pp 211–248. https://doi.org/10.1007/978-0-387-70805-8_8
- Schroder P, Herzog R, Bojinov B, Ruttens A, Nehnevajova E, Stamatidis S, Memon A, Vassilev A, Caviezel M, Vangronsveld J. Bioenergy to save the world. Producing novel energy plants for growth on abandoned land. *Environ Sci Pollut Res.* 2008;15:196–204. <https://doi.org/10.1065/espr2008.03.481>.
- Scully ED, Gries T, Palmer NA, Sarath G, Funnell-Harris DL, Baird L, Twigg P, Seravalli J, Clemente TE, Sattler SE. Overexpression of SbMyb60 in Sorghum bicolor impacts both primary and secondary metabolism. *New Phytol.* 2018;217(1):82–104. <https://doi.org/10.1111/nph.14815>.
- Shen B, Sun X, Zuo X, Shilling T, Apgar J, Ross M, Bougri O, Samoylov V, Parker M, Hancock E, Lucero H. Engineering a thermoregulated intein-modified xylanase into maize for consolidated lignocellulosic biomass processing. *Nat Biotechnol.* 2012a;30(11):1131–6. <https://doi.org/10.1038/nbt.2402>.
- Shen H, He X, Poovaiah CR, Wuddineh WA, Ma J, Mann DG, Wang H, Jackson L, Tang Y, et al. Functional characterization of the switchgrass (*Panicum virgatum*) R2R3-MYB transcription factor PvMYB4 for improvement of lignocellulosic feedstocks. *New Phytologist.* 2012;193(1):121–36. <https://doi.org/10.1111/j.1469-8137.2011.03922.x>.
- Shen H, Poovaiah CR, Ziebell A, Tschaplinski TJ, Pattathil S, Gjersing E, Engle NL, Katahira R, Pu Y, Sykes R, Chen F. Enhanced characteristics of genetically modified switchgrass (*Panicum virgatum* L.) for high biofuel production. *Biotechnol Biofuels.* 2013;6(1):1–5. <https://doi.org/10.1186/1754-6834-6-71>.
- Sheykhbaglou R, Sedghi M, Shishevan MT, Sharifi RS. Effects of nano-iron oxide particles on agronomic traits of soybean. *Notulae Scientia Biologicae.* 2010;2(2):112–3. <https://doi.org/10.15835/nsb224667>.
- Shim D, Kim S, Choi YI, Song WY, Park J, Youk ES, Jeong SC, Martinoia E, Noh EW, Lee Y. Transgenic poplar trees expressing yeast cadmium factor 1 exhibit the characteristics necessary for the phytoremediation of mine tailing soil. *Chemosphere.* 2013;90:1478–86. <https://doi.org/10.1016/j.chemosphere.2012.09.044>.

- Singh A, Prajapati P, Vyas S, Gaur VK, Sindhu R, Binod P, Kumar V, Singhania RR, Awasthi MK, Zhang Z, Varjani S. A comprehensive review of feedstocks as sustainable substrates for next-generation biofuels. *BioEnergy Res.* 2023;16(1):105–22. <https://doi.org/10.1007/s12155-022-10440-2>.
- Skinner DZ, Muthukrishnan S, Liang GH. Transformation: A powerful tool for crop improvement. In: Skinner DZ, Liang GH, editors. *Genetically Modified Crops: Their Development, Uses, and Risks*. New York: Food Products Press; 2004. p. 1–16.
- Slavov GT, Nipper R, Robson P, Farrar K, Allison GG, Bosch M, Clifton-Brown JC, Donnison IS, Jensen E. Genome-wide association studies and prediction of 17 traits related to phenology, biomass and cell wall composition in the energy grass *Miscanthus sinensis*. *New Phytol.* 2014;201:1227–2123. <https://doi.org/10.1111/nph.12621>.
- Sticklen MB. Plant genetic engineering for biofuel production: towards affordable cellulosic ethanol. *Nat Rev Genet.* 2008;9(6):433–43. <https://doi.org/10.1038/nrg2336>.
- Sun JY, Hammerlindl J, Forseille L, Zhang H, Smith MA. Simultaneous over-expressing of an acyl-ACP thioesterase (F at B) and silencing of acyl-acyl carrier protein desaturase by artificial micro RNA s increases saturated fatty acid levels in *Brassica napus* seeds. *Plant Biotechnol J.* 2014;12(5):624–37. <https://doi.org/10.1111/pbi.12168>.
- Suo H, Ma Q, Ye K, Yang C, Tang Y, Hao J, Zhang ZJ, Chen M, Feng Y, Nian H. Overexpression of AtDREB1A causes a severe dwarf phenotype by decreasing endogenous gibberellin levels in soybean [*Glycine max* (L.) Merr]. *PLoS One.* 2012;5(7):e12142. <https://doi.org/10.1371/journal.pone.0045568>.
- Tester M, Langridge P. Breeding technologies to increase crop production in a changing world. *Science.* 2010;327:818–22. <https://doi.org/10.1126/science.1183700>.
- Tew TL, Cobill RM. Genetic improvement of sugarcane (*Saccharum* spp.) as an energy crop. In: Vermerris W, editor. *Genetic Improvement of Bioenergy Crops*. New York: Springer; 2008. p. 249–72.
- Tian N, Wang J, Xu ZQ. Overexpression of Na⁺/H⁺ antiporter gene AtNHX1 from *Arabidopsis thaliana* improves the salt tolerance of kiwifruit (*Actinidia deliciosa*). *S Afr J Bot.* 2011;77(1):160–9. <https://doi.org/10.1016/j.sajb.2010.07.010>.
- Torney F, Moeller L, Scarpa A, Wang K. Genetic engineering approaches to improve bioethanol production from maize. *Curr Opin Biotechnol.* 2007;18:193–9. <https://doi.org/10.1016/j.copbio.2007.03.006>.
- Tschaplinski TJ, Standaert RF, Engle NL, Martin MZ, Sangha AK, Parks JM, Smith JC, Samuel R, Jiang N, Pu Y, Ragauskas AJ. Down-regulation of the caffeic acid O-methyltransferase gene in switchgrass reveals a novel monolignol analog. *Biotechnol Biofuels.* 2012;5:1–15. <https://doi.org/10.1186/1754-6834-5-71>.
- Tuskan GA, Difazio S, Jansson S, Bohlmann J, Grigoriev I, Hellsten U, Putnam N, Ralph S, Rombauts S, Salamov A, Schein J. The genome of black cottonwood, *Populus trichocarpa* (Torr. & Gray). *Science.* 2006;313:1596–604. <https://doi.org/10.1126/science.1128691>.
- Ullmann J, Grimm D. Algae and their potential for a future bioeconomy, landless food production, and the socio-economic impact of an algae industry. *Org Agric.* 2021;11(2):261–7. <https://doi.org/10.1007/s13165-020-00337-9>.
- Umakanth, A.V., Datta, A., Reddy, B.S. and Bardhan, S., 2022. Biomass feedstocks for advanced biofuels: Sustainability and supply chain management. *Advanced Biofuel Technologies*, pp.39–72. <https://doi.org/10.1016/B978-0-323-88427-3.00023-4>
- Vanholme R, Morreel K, Darrah C, Oyarce P, Grabber JH, Ralph J, Boerjan W. Metabolic engineering of novel lignin in biomass crops. *New Phytol.* 2012;196(4):978–1000. <https://doi.org/10.1111/j.1469-8137.2012.04337.x>.
- Vega-Sánchez ME, Ronald PC. Genetic and biotechnological approaches for biofuel crop improvement. *Curr Opin Biotechnol.* 2010;21(2):218–24. <https://doi.org/10.1016/j.copbio.2010.02.002>.
- Voelker SL, Lachenbruch B, Meinzer FC, Jourdes M, Ki C, Patten AM, Davin LB, Lewis NG, Tuskan GA, Gunter L, Decker SR. Antisense down-regulation of 4CL expression alters lignification, tree growth, and saccharification potential of field-grown poplar. *Plant Physiol.* 2010;154(2):874–86. <https://doi.org/10.1104/pp.110.159269>.
- Wallace J, Larsson S, Buckler E. Entering the second century of maize quantitative genetics. *Heredity.* 2014;112:30–8. <https://doi.org/10.1038/hdy.2013.6>.
- Wang YC, Qu GZ, Li HY, Wu YJ, Wang C, Liu GF, Yang CP. Enhanced salt tolerance of transgenic poplar plants expressing a manganese superoxide dismutase from *Tamarix androssowii*. *Mol Biol Rep.* 2010;37:1119–24. <https://doi.org/10.1007/s11033-009-9884-9>.
- Wang Y, Fan C, Hu H, Li Y, Sun D, Wang Y, Peng L. Genetic modification of plant cell walls to enhance biomass yield and biofuel production in bioenergy crops. *Biotechnol Adv.* 2016;34(5):997–1017. <https://doi.org/10.1016/j.biotechadv.2016.06.001>.
- Wang HM, Yuan TQ, Song GY, Sun RC. Advanced and versatile lignin-derived biodegradable composite film materials toward a sustainable world. *Green Chem.* 2021;23(11):3790–817. <https://doi.org/10.1039/D1GC00790D>.
- Whitaker J, Field JL, Bernacchi CJ, Cerri CE, Ceulemans R, Davies CA, DeLucia EH, Donnison IS, McCalmont JP, Paustian K, Rowe RL. Consensus, uncertainties and challenges for perennial bioenergy crops and land use. *GCB Bioenergy.* 2018;10(3):150–64. <https://doi.org/10.1111/gcbb.12488>.
- Wilas J, Maśniak R, Daniszewski P, Jadczyk P. Renewable energy sources today and tomorrow. *World Sci News.* 2016;60:103–12.
- Wilkerson CG, Mansfield SD, Lu F, Withers S, Park JY, Karlen SD, Gonzales-Vigil E, Padmakhan D, Unda F, Rencoret J, Ralph J. Monolignol ferulate transferase introduces chemically labile linkages into the lignin backbone. *Science.* 2014;344:90–3. <https://doi.org/10.1126/science.1250161>.
- Windhausen VS, Wagener S, Magorokosho C, Makumbi D, Vivek B, Piepho HP, Melchinger AE, Atlin GN. Strategies to subdivide a target population of environments: results from the CIMMYT-led maize hybrid testing programs in Africa. *Crop Sci.* 2012;52:2143–52. <https://doi.org/10.2135/cropsci2012.02.0125>.
- Wu L, Birch RG. Physiological basis for enhanced sucrose accumulation in an engineered sugarcane cell line. *Funct Plant Biol.* 2010;37:1161–74. <https://doi.org/10.1071/FP10055>.
- Xu Y, Lu Y, Xie C, Gao S, Wan J, Prasanna BM. Whole-genome strategies for marker-assisted plant breeding. *Mol Breed.* 2012;29:833–54. <https://doi.org/10.1007/s11032-012-9699-6>.
- Yadav, P., Priyanka, P., Kumar, D., Yadav, A. and Yadav, K., 2019. Bioenergy crops: recent advances and future outlook. *Prospects of renewable bioprocessing in future energy systems*, pp.315–335. https://doi.org/10.1007/978-3-030-14463-0_12
- Yuan JS, Tiller KH, Al-Abmad H, Stewart NR, Stewart NS. Plants to power: bioenergy to fuel the future. *Trends Plant Sci.* 2008;13:421–9. <https://doi.org/10.1016/j.tplants.2008.06.001>.
- Zhang Y, Maximova SN, Guiltinan MJ. Characterization of a stearoyl-acyl carrier protein desaturase gene family from the chocolate tree, *Theobroma cacao* L. *Front Plant Sci.* 2015;6:239. <https://doi.org/10.3389/fpls.2015.00239>.
- Zhao F, Yang W, Zeng Z, Li H, Yang X, He Z, Gu B, Rafiq MT, Peng H. Nutrient removal efficiency and biomass production of different bioenergy plants in hypereutrophic water. *Biomass Bioenergy.* 2012;42:212–8. <https://doi.org/10.1016/j.biombioe.2012.04.003>.
- Zhou M, Li D, Li Z, Hu Q, Yang C, Zhu L, Luo H. Constitutive expression of a miR319 gene alters plant development and enhances salt and drought tolerance in transgenic creeping bentgrass. *Plant Physiol.* 2013;161(3):1375–91. <https://doi.org/10.1104/pp.112.208702>.
- Zhou X, Jacobs TB, Xue LJ, Harding SA, Tsai CJ. Exploiting SNPs for biallelic CRISPR mutations in the outcrossing woody perennial *Populus* reveals 4- coumarate: CoA ligase specificity and redundancy. *New Phytol.* 2015;208:298–301. <https://doi.org/10.1111/nph.13470>.
- Zou Z, Yang J. Genome-wide comparison reveals divergence of cassava and rubber aquaporin family genes after the recent whole-genome duplication. *BMC Genomics.* 2019;20:1–16. <https://doi.org/10.1186/s12864-019-5780-4>.
- Zou G, Zhai G, Feng Q, Yan S, Wang A, Zhao Q, Shao J, Zhang Z, Zou J, Han B, Tao Y. Identification of QTLs for eight agronomically important traits using an ultra-high-density map based on SNPs generated from high-throughput sequencing in sorghum under contrasting photoperiods. *J Exp Bot.* 2012;63:5451–62. <https://doi.org/10.1093/jxb/ers205>.

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