

Optimizing root system architecture in biofuel crops for sustainable energy production and soil carbon sequestration

Jennifer PC To¹, Jinming Zhu¹, Philip N Benfey^{1,2} and Tedd Elich^{1*}

Addresses: ¹GrassRoots Biotechnology, 302 E Pettigrew Street, Suite A200, Durham, NC 27701, USA; ²Department of Biology and IGSP Center for Systems Biology, Duke University, Durham, NC 27708, USA

* Corresponding author: Tedd Elich (tedd.elich@grassrootsbio.com)

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Abstract

Root system architecture (RSA) describes the dynamic spatial configuration of different types and ages of roots in a plant, which allows adaptation to different environments. Modifications in RSA enhance agronomic traits in crops and have been implicated in soil organic carbon content. Together, these fundamental properties of RSA contribute to the net carbon balance and overall sustainability of biofuels. In this article, we will review recent data supporting carbon sequestration by biofuel crops, highlight current progress in studying RSA, and discuss future opportunities for optimizing RSA for biofuel production and soil carbon sequestration.

Introduction and context

Carbon dioxide (CO₂) is the major anthropogenic greenhouse gas (GHG) and its atmospheric concentration has risen by approximately 100 parts per million since the Industrial Revolution. With current CO₂ accumulation rates, global temperatures are predicted to increase between 1.4°C and 5.8°C by the end of this century [1]. Fossil fuel consumption releases carbon (C) from underground stores into the atmosphere and is a major contributor to the increase of GHG. In contrast, biofuels can be considered C-neutral or C-negative because the majority of C emitted from their consumption is fixed from ambient CO₂. However, estimates of GHG balances from biofuel crop production vary from C-negative to C-positive depending on the assumptions, components, and boundaries used in the analysis [2]. The uncertainties that contribute to these variable estimates include GHG emissions from energy inputs during crop production and biofuel processing as well as terrestrial C loss due to converting land to agriculture. Furthermore, biofuel crop cultivation may raise land use issues, including competition with food production and destruction of natural habitats [3]. What is clear from these studies is that the sustainability of biofuels

depends on the availability of feedstocks that can grow on low-quality soils like abandoned farmland, are productive with minimal energy inputs, and can potentially increase soil organic carbon (SOC) accumulation [4].

Root system architecture (RSA) describes the spatial configuration of different types and ages of roots in a plant. RSA is highly plastic and varies with growth conditions to allow soil exploration for nutrients; variation in RSA is found between species and between varieties within a species that are adapted to different environments [5]. In agricultural crops, RSA has been shown to enhance yield, drought tolerance, and nutrient efficiency, which can increase productivity and reduce input requirements [6-9]. For optimal growth on marginal lands, biofuel crop RSA should promote shallow adventitious roots and dispersed lateral roots to forage topsoils for diffusion-limited nutrients and reduce runoff on steep grades as well as deeper roots to increase water and soluble nutrient uptake [9]. Furthermore, root tissue and exudates contribute to terrestrial C pools. Increasing root biomass, in particular with deeper roots, has been predicted to increase C sequestration

because C loss due to microbial decomposition is concentrated in the upper soil strata [10].

Herbaceous perennial grasses such as switchgrass and *Miscanthus* can grow on marginal lands, efficiently fix C, and reduce net CO₂ emissions through C sequestration in deep roots [11]. Low-input, high-diversity perennial grasses grown for biofuels have been estimated to sequester 4.85 tons/hectare per year of CO₂, while current corn grain ethanol and soybean diesel are C-positive [12,13]. Despite these attributes, perennial grasses have not been widely adopted commercially because cellulosic ethanol is not cost-competitive with fossil fuels in the current market [14,15]. Increasing the agronomic productivity and environmental benefits of biofuel crops by modifying RSA can facilitate the entry of biofuels into the marketplace.

Major recent advances

Changes in soil organic carbon under biofuel crops

A large-scale switchgrass field study recently reported net energy gains of cellulosic ethanol and increase in SOC [16,17]. This study was conducted on 10 farms averaging 6.7 hectares across a 930-km latitude range in the central and northern Great Plains in the US. SOC underwent significant increases: 4.0 megagrams of CO₂/hectare per year at a soil depth of 0-30 cm and 10.6 megagrams of CO₂/hectare per year at a soil depth of 0-120 cm [17]. Another recent study re-analyzed changes in soil organic C under biofuel feedstock cultivation across a set of 46 experiments representing 146 site treatment combinations [18]. These experiments tested four types of biofuel feedstocks (corn stover, sugarcane, *Miscanthus*, and switchgrass) and mixed native prairie grasses. All feedstocks, except corn stover, were correlated with an increase in SOC. Notably, *Miscanthus* and switchgrass were estimated to increase SOC by 5-25% at a soil depth of 0-60 cm in 5-20 years. Sugarcane plots were found to accumulate SOC in smaller amounts and at shallower depths than switchgrass. Mixed native grasses that were not harvested for biofuel production were predicted to have the highest potential to accumulate SOC [18]. The results were complicated by the effects of site soil characteristics, management practices, and climate. Nonetheless, the results were generally consistent with predictions that SOC would decrease as a result of conversion of native ecosystems to agricultural use, and that SOC would accumulate as a result of conversion of farmland to grassland. [19]. Globally, there are approximately 400 megahectares of abandoned farmland that have not been converted to other uses [20]. Cultivating perennial grasses on this land for energy crop production is projected to sequester up to 1.9 gigatons/year of CO₂.

Phenotyping and optimizing root system architecture in biofuel crops

Functional RSA traits for biofuel feedstocks, including increased root depth and branching, are proposed to increase productivity on marginal land and promote C sequestration [9,10]. These root traits have been referred to as traits of the second Green Revolution because they enhance crop tolerance to drought and low-nutrient conditions that are prevalent in the developing world [9]. Unfortunately, owing to high-input conditions used during selection as well as the difficulty of observing underground tissues, these traits have often been neglected in traditional programs for breeding. Recent implementation of noninvasive *in vivo* root imaging systems such as gel-based optical imaging [21], X-ray imaging [22], nuclear magnetic resonance [23], and short-lived radioisotope imaging [24] is expediting efforts to characterize RSA traits. Further advances in automating image capture and analysis methods have been reported in *Arabidopsis* and rice [21,25] and will facilitate genome-wide identification of RSA traits in biofuel crops.

While recent studies support perennial grasses for efficient soil C sequestration [16-18], they also raise the issue of a trade-off in C allocations aboveground and belowground, which contribute to biofuel crop productivity and SOC accumulation, respectively [18,26]. In addition, SOC has been correlated with levels of nitrogen [19,27], likely in part through modulation of plant C cycles and RSA. Efforts to optimize RSA for nitrogen uptake efficiency can potentially increase C sequestration capabilities. Understanding how plants respond to C and nitrogen inputs in variable environments and how these inputs are allocated into shoot biomass aboveground for harvest and root biomass belowground for C sequestration are interesting research areas for biofuel crop improvement.

Genetic control of root system architecture in grasses

Studies on genetic determinants of RSA have been pursued largely in the model dicot *Arabidopsis* as well as in the cereals rice and maize (reviewed in [28-31]). In *Arabidopsis*, RSA is defined by iterative development of lateral roots beginning on the radicle-derived primary root. *Arabidopsis* lateral root development, from initiation through patterning events after emergence, is coordinated largely by the phytohormones auxin and cytokinin [29,30,32]. Elongation of primary and lateral roots is mediated by both cell division and cell expansion control, including cell wall biosynthesis and modification mechanisms [30,33]. Adaptive RSA results from lateral root development and directional root elongation responses to environmental signals such as nutrient

levels and mechanical stimuli, which are modulated in part by phytohormones [34,35]. Rice, maize, and other monocots generate a more complex fibrous root system that includes embryonic primary and seminal roots, postembryonic soil-borne or air-borne adventitious roots, and lateral roots that arise from all of the aforementioned types. Recent cloning of a number of genes mutated in rice and maize root branching-defective mutants has identified genes involved in polarized auxin transport and response and identified cytokinin response pathways [29,30] and transcription factors, including auxin-inducible LATERAL ORGAN BOUNDARY transcription factors in maize [36] and rice [37] and a cytokinin-regulated WUSCHEL-related homeobox gene in rice [38]. These findings suggest that conservation in root branching mechanisms between monocots and dicots persists despite major differences in RSA and lend support to comparative genomic approaches.

In perennial grasses, the study of RSA genes is in its infancy and this is primarily due to their large and complex genomes. Recently, genome sequencing of the cultivated grass *Sorghum bicolor* [39] and the wild grass *Brachypodium distachyon* [40] has been completed, and genome sequencing of proposed biofuel feedstocks foxtail millet and switchgrass is under way. Comparative genomics has identified homologs and regions of synteny between these grasses [40-43], and these regions will facilitate identification of orthologous gene sets involved in RSA in biofuel crops.

A recent major breakthrough in Arabidopsis root development was the identification of microRNAs (miRNAs) that regulate lateral root branching and root patterning [44-46]. Genomic approaches have identified miRNAs in maize [47-49], rice [50], *Brachypodium* [51,52], and switchgrass [53]. Artificial miRNAs have been used to modulate gene expression in many experimental systems [54], and understanding miRNAs in grasses can potentially develop this tool for manipulating RSA in biofuel crops.

Global transcriptional profiling experiments using microarrays have identified rice genes responsive to environmental changes in nitrogen and water stress conditions [55,56]. A high-resolution transcriptional map of the rice root and gene expression profiles of several maize root cell types (wild-type and mutant) that regulate root branching have been generated by means of laser capture microdissection [57,58]. Comparison of these gene expression profiles with high-resolution gene expression profiles generated from Arabidopsis [59] implicates sets of common and distinct genetic mechanisms in RSA determination.

Quantitative trait loci (QTLs) mapping in rice and maize is ongoing, and many QTLs controlling root traits in rice and maize have been identified but none has yet been cloned [6,28,29]. The gene expression data will also inform RSA candidate gene prioritization in QTLs in the future. Genetic tools in biofuel crops, including germplasms of natural accessions, recombinant- and near-inbred line populations, mutants, and genetic and physical maps as well as genetic transformation methods, are being developed to advance trait identification in biofuel crops [60-63].

Future directions

Genetic tools, as mentioned above, including germplasms of natural accessions and mutants as well as genetic and physical maps of biofuel crops, are currently being developed. These tools, coupled with large-scale phenotyping and genotyping pipelines, will expedite discovery of RSA traits and genes for breeding and genetic manipulation to generate improved C-negative biofuel crops with sustainable biomass production.

Abbreviations

C, carbon; CO₂, carbon dioxide; GHG, greenhouse gas; miRNA, microRNA; QTL, quantitative trait locus; RSA, root system architecture; SOC, soil organic carbon.

Competing interests

GrassRoots Biotechnology is a for-profit organization that conducts research to enhance agricultural and biofuel crops. We apologize to any colleagues whose work was excluded because of space constraints.

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