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Review article

High-biomass C_4 grasses—Filling the yield gap[☆]

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ABSTRACT

A significant increase in agricultural productivity will be required by 2050 to meet the needs of an expanding and rapidly developing world population, without allocating more land and water resources to agriculture, and despite slowing rates of grain yield improvement. This review examines the proposition that high-biomass C_4 grasses could help fill the yield gap. High-biomass C_4 grasses exhibit high yield due to C_4 photosynthesis, long growth duration, and efficient capture and utilization of light, water, and nutrients. These C_4 grasses exhibit high levels of drought tolerance during their long vegetative growth phase ideal for crops grown in water-limited regions of agricultural production. The stems of some high-biomass C_4 grasses can accumulate high levels of non-structural carbohydrates that could be engineered to enhance biomass yield and utility as feedstocks for animals and biofuels production. The regulatory pathway that delays flowering of high-biomass C_4 grasses in long days has been elucidated enabling production and deployment of hybrids. Crop and landscape-scale modeling predict that utilization of high-biomass C_4 grass crops on land and in regions where water resources limit grain crop yield could increase agricultural productivity.

1. Challenges and strategies for increasing agricultural productivity

1.1. Critical need and time frame assessment

World population increased from ~1.8 B in 1900 to ~7.1 B in 2013 and is projected to exceed ~9 B by 2050. Population growth and rapid development are driving increased demand for food, animal feed, bioenergy, and other bio-products derived from agriculture creating an ongoing need for increased agricultural productivity [1]. Higher protein diets associated with rising standards of living increase the demand for agricultural products because animals convert plant feedstocks into protein at ratio's ranging from ~2:1 to ~4:1. Efforts to increase energy independence, reduce energy costs, and increase environmental sustainability have led to increased production of biofuels over the past decade, primarily from grain. In the U.S., these trends have resulted in ~80% of agricultural production [2] and ~80% of the maize grain crop [3] being used for animal feed and production of biofuels. Longer term, agriculture may also need to generate some of the hydrocarbons used in the petrochemical industry when economically recoverable supplies of these feedstocks from geological sources are depleted.

Over the past century, the need for increased production of food, animal feed, fiber, and other products derived from crops was met by allocating more land to agricultural production, increasing inputs, optimizing crop management and improving crop genetics. Intensification of agricultural production has been accompanied by increased use of water resources, nitrogen fertilizers, and chemicals that control weeds and pests, intensive crop management, and the development of crops with biotechnology-enhanced traits such as herbicide tolerance and pest resistance. Despite substantial increases in crop productivity over the past 75 years, it is estimated that output needs to increase an additional ~60-110% by 2050 [1]. Given this situation, the slowing rate of grain yield improvement of rice, wheat, and corn, the major sources of calories for the human population, and the emergence of yield plateaus [4–6], is of great concern. Following an overview of constraints, challenges, and opportunities associated with increasing grain crop yield, this review will examine the potential for high-biomass C_4 grass crops to increase agricultural productivity in water-limited regions of production.

1.2. Land and water resource constraints on grain crop yield

The most useful land for agriculture is already in production spanning nearly 38% of the Earth's land surface area [7]. Allocation of more marginal land to agriculture will yield less, encroach on wildlife habitats that are sources of valuable biodiversity, and risk disruption of ecosystem sustainability [7]. Agriculture uses 2600 km^3 of water each year mainly for irrigation, nearly two-thirds of all water used by humans [8]. Irrigation is critical for high crop productivity

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[☆] In this review, gene names are capitalized and italicized (i.e., *EHD1*), and protein products derived from genes are not italicized (i.e., Ehd1).

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because insufficient water supply is one of the most significant constraints on grain yield especially when water-deficit occurs during the reproductive phase [9,10]. Development and deployment of more efficient irrigation systems that optimize the application, timing, and amount of irrigation to minimize run-off and evaporation could increase yield by utilizing water supplies more effectively. In many rain-fed regions of crop production that lack access to supplemental irrigation, limited water supplies reduce yield to some extent annually, and drought periodically causes severe disruption of grain production [10]. In the future water supplies for agriculture are likely to become more restricted due to competition from urban centers and industry and because many historical sources of water used for crop production will be depleted within this century [8]. In addition, climate variation could increase the frequency of drought in some highly productive agricultural regions. Taken together, this indicates that a significant increase in agricultural productivity will be required using land and water resources currently available for this activity to meet the needs of a growing world population that is undergoing rapid development.

1.3. Lessons from the history of grain yield improvement

Grain is a highly valued agricultural product because seeds accumulate readily digested starch, oils, and proteins at high density and store these products in a stable low moisture state that is ideal for harvesting, transport, storage, and utilization. Efforts to improve grain yield have been underway since crop domestication began thousands of years ago. Improvements in grain yield are the result of increases plant biomass yield and/or harvest index [5]. Retrospective analysis indicates that grain harvest index has been under strong selection in the major cereal crops, reaching an apparent maximum of ~55-60%. More recent improvements in grain yield are correlated with increased plant biomass yield with relatively small changes in harvest index. Increases in grain crop biomass yield have occurred primarily through selection for higher growth rates, increased planting densities resulting in improved radiation interception, improved radiation use efficiency, maintenance of high rates of photosynthesis during grain filling (i.e., functional stay green), and better adaptation to water-limited environments among other traits [5].

Cereal crop yield has plateaued in some of the world's most productive agricultural regions [6] indicating that opportunities for increasing grain crop productivity are becoming more limited as would be expected following a century of yield improvement. The decreasing rate of grain yield improvement indicates that genetic improvement of grain crops and associated crop management practices may be reaching limits that will be difficult to overcome without fundamental changes in plant photochemistry, the enzymology of CO_2 fixation, and/or the linkage between CO_2 uptake for photosynthesis and water loss through transpiration. The sensitivity of grain yield to water-deficit during the reproductive phase is a particularly important constraint that decreases yield, increases risk, and impacts where grain crops are grown. Plants adjust the number of seed set based on plant carbon and nitrogen status early in the reproductive phase ensuring that some viable seed are produced [11,12]. As a consequence, grain yield is very sensitive to water-deficit during the reproductive phase because this constraint has a negative impact on photosynthesis and carbon status and nitrogen uptake and assimilation [9,10]. Stay-green traits that reduce canopy size [13] and mechanisms that limit transpiration under conditions of high vapor pressure deficit (VPD) [14,15], shift water use and biomass accumulation from the vegetative to reproductive phase improving grain yield in water-limited environments. Traits that increase biomass partitioning to seeds by reducing the growth of leaves and stems post floral initiation and/or that modify carbon-status/signaling/sink strength by altering production of trehalose-6-phosphate [16] and ethylene [17] have also been successful in increasing grain yield in water-limited environments. However, these traits are unlikely to allow a significant extension of grain crop growth duration in water-limited environments without associated increases in risk. This is because an inherent property of grain production is the relative inflexibility of grain crop development relative to variation in the timing and duration of environmental constraints that occur each season. To manage risk while maximizing yield, grain crop genotypes with specified flowering times are utilized for each region of production based on average season length and climate constraints. Once grain crops undergo floral initiation, the time to flowering, and the interval from anthesis to grain maturity are relatively constant (i.e., ~30 days each for grain sorghum). The selection of grain crop genotypes with defined flowering times reduces grain yield in years when adverse environmental constraints occur during the reproductive phase and minimizes the potential for greater yield through season extension in years with more optimal growing conditions. In contrast, high-biomass C4 grasses that can tolerate water-deficit and other constraints during a long duration vegetative growth phase have the potential for higher biomass accumulation in years with good growing conditions.

1.4. Emerging opportunities for increasing crop productivity

Crop productivity and utility can be increased by: (i) improving the fundamental genetic potential of plants to capture light energy, carry out carbon fixation, and to accumulate biomass under good growing conditions; (ii) enhancing crop resilience to biotic and abiotic constraints that reduce plant productivity in sub-optimal environments; (iii) improving crop management, nutrient/water inputs, and weed and pest control; (iv) optimizing the deployment of crops and other plants within and across regions of agricultural production; and (v) by increasing sink strength and altering the partitioning and composition of accumulated plant biomass to enhance yield, improve the logistics of harvesting, transport, storage, and processing, and increase end-product value. Recent advances in high-throughput phenotyping, multi-scale modeling, low cost genotyping, and gene-editing technology have the potential to significantly increase the productivity and value of crops. A key question is how best to utilize these new technologies for that purpose.

Advanced phenomic platforms generate large geo-referenced datasets comprised of plant/field images, hyper-spectral or multi-spectral information, and environmental data that can be used to assess rates of biomass accumulation, leaf area, nitrogen, and water content, onset of biotic and abiotic constraints, and yield with high temporal and spatial resolution [18]. Automated phenotyping technology can be used to help screen large numbers of crop genotypes, identify genetic determinants of crop productivity, and characterize genotype by environment interactions. This technology, in conjunction with genotyping-by-sequencing methods, has the potential to synergize efforts to improve crops through the selection of optimal combinations of naturally occurring gene variants and trait improvement through gene-editing and pathway/trait engineering.

To take full advantage of these emerging technologies and their potential for increasing the rate of crop improvement, there is a critical need to identify the crops, plant functions/traits, and crop management practices that could have the largest impact on crop yield if further optimized. One approach combines knowledge gained from fundamental research on photosynthesis and employs modeling to identify canopy architecture traits, photochemical processes, and biochemical reactions that could be modified to improve plant productivity [19]. For maximum impact, improvements in photosynthetic efficiency need to be combined with increases in sink strength and resilience to biotic and abiotic constraints. Collection of data at field and regional scales combined with crop and landscape modeling allows the identification of constraints operating at higher levels of organization and traits/management solutions that could minimize these constraints [20–22]. This modeling approach indicates there are unexploited opportunities for improving the productivity of agricultural systems associated with more optimal deployment of current and new types of crops such as