



## Review

## Plant science and agricultural productivity: Why are we hitting the yield ceiling?

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## ARTICLE INFO

## Article history:

Received 9 February 2013

Received in revised form 26 April 2013

Accepted 16 May 2013

Available online 23 May 2013

## Keywords:

Biomass

Biological productivity

Eco-evo-devo

Growth rate

Heterosis

Organ growth

Photosynthesis

Soil

Sustainable agriculture

Water

Yield ceiling

## ABSTRACT

Trends in conventional plant breeding and in biotechnology research are analyzed with a focus on production and productivity of individual organisms. Our growing understanding of the productive/adaptive potential of (crop) plants is a prerequisite to increasing this potential and also its expression under environmental constraints. This review concentrates on growth rate, ribosome activity, and photosynthetic rate to link these key cellular processes to plant productivity. Examples of how they may be integrated in heterosis, organ growth control, and responses to abiotic stresses are presented. The yield components in rice are presented as a model. The ultimate goal of research programs, that concentrate on yield and productivity and integrating the panoply of systems biology tools, is to achieve “low input, high output” agriculture, i.e. shifting from a conventional “productivist” agriculture to an efficient sustainable agriculture. This is of critical, strategic importance, because the extent to which we, both locally and globally, secure and manage the long-term productive potential of plant resources will determine the future of humanity.

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## 1. Introduction

Plants are the engines of terrestrial (agro)-ecosystems. Primary photosynthetic production sets the absolute upper limit for all heterotrophs and present agricultural production [1]. Plants also sequester carbon, and operate as factories producing diverse chemicals, and plant ecosystems serve as water reservoirs. These properties have been used by humans to produce an extremely productive agriculture in the past millennium.

Domestication by our preliterate ancestors achieved spectacular results, through critical selection of modifications to morphology, physiology, and biochemistry of plants and animals. Further modifications of comparable ingenuity may be required for the needed increases in production (see Section 7). Plant breeding has been historically oriented toward high agronomic yield, disease and pest resistance, easy and consistent processing, and traits advantageous for cultivation and business. In conventional modern agriculture, the Green Revolution is considered “*the first systematic, large-scale attempt to reduce poverty and hunger across the world*” by substantially increasing production [2]. The recipe for this was an assortment of high yielding, water- and/or fertilizer-responsive varieties, irrigation, pesticides and fertilizer use [3].

What has been the contribution of ag-biotech? A report prepared by a USDA A21 committee shows that yield security is a main target of ag-biotech [4]. The first two classes of products of crop biotechnology, broad-spectrum herbicide-tolerant and Bt-mediated insect resistance crops in corn, cotton, canola and soybeans (i.e., crops with large seed markets), have been widely adopted in the U.S, Canada, South America, India and China because such traits have not been generated through classical breeding. By 2012, more than 10% of the world crop lands were growing transgenic crops, with an annual growth rate of 6% [5]. The new varieties essentially provided increased profitability [6], and, as a collateral benefit, reduced pesticide use and better conservation tillage. Near-term applications offer resistance to viruses, pathogens and insects, and improved processing and storage [7,8].

Despite such spectacular advances in the past, we now seem to be reaching yield ceilings in several major crops and the increase of global relative crop yields is slowing down [9,10]. While some local potential for yield increase is recognized in Africa and SE Asia, the fundamental causes of this levelling off include lack of genetic diversity for breeding programs, including the numbers of species used, climate instability, cultural practices, soil and environmental degradation, losses of agricultural land, and economic constraints (and in particular under-investment in agriculture since the end of the 1980s) [3,9,11]. For example, today 80% of calories for humans and livestock come from only four species [9]. The need for a second green revolution is advocated by experts [3,12], and institutions, such as FAO [13], with strong emphasis on research towards: (1) the

understanding of mechanisms by which genetic variation, genome architecture, and environmental cues and changes can modify yield; (2) shifting breeding goals towards more environmentally-friendly agriculture. These approaches require a much broader thinking in both science and society than before.

## 2. Conventional genetic yield improvement methods in agriculture

Crop productivity presently combines the effects of the domestication and refinement of crops by pre-scientific peoples, along with two centuries of breeding programs, partly informed by genetic knowledge. Both stages in the development of agriculture are important because in both cases humans have affected the strength and the direction of selection. The biggest changes to plant architecture and morphology happened in the former period. For example, maize is so different from its ancestor teosinte that the origin of maize from teosinte was long disputed [14]. Seen the time scale of the domestication “age”, agriculture has produced a large number of early domesticated species that could deal with various kinds of stresses at a time (also see [15]). Intentional and continuous breeding programs now produce new varieties in short periods of time [16].

Understanding how human selection drives evolution through domestication and breeding is important in revealing what drives such rapid adaptation in man-made environments [17]. Field management practices and biotic or abiotic environmental factors are largely contributing to selection pressure on a target species resulting in accelerated changes in genome structure compared with its wild ancestor. A remarkable example: weeds are under strong selection to evolve seeds that mimic the crop in size, shape, and phenology (termed “crop mimicry”) allowing weed seeds to be harvested by the farmer and replanted in subsequent years. The ancestors of rye and later oats began as weeds in grain fields, and through this process became cultivated crops themselves [18].

The dramatic increase in yield in crops, such as hybrid maize and rice, required engineering valuable agronomic complex traits through an assortment of breeding technologies together with processes such as hybridization, polyploidization, and reproductive fitness, which are detailed below.

### 2.1. Hybridization and introgression

Hybridization and introgression have been important since ancient times, but became more important with scientific plant breeding in the 20th century, culminating in the use of heterosis and cytoplasmic male sterility in breeding programs. It is estimated that one out of four cultivated plant species carry introgressed alleles from another species [19].

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