Plant Science 210 (2013) 159–176

Contents lists available at SciVerse ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

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.

Contents

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http://dx.doi.org/10.1016/j.plantsci.2013.05.010

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].

Crop–wild progenitor comparisons are ideal for studying the evolution of novel adaptations, in particular when crops spread out from their centres of origin; examples are wheat, *Brassica*, and maize for adaptation to new light regimes or more generally for pathogen-resistance traits [19,20]. Chromosome doubling in interspecific hybrids (see Section 6.1) allows hybrid vigour to become permanently fixed [21].

2.2. Polyploidy

Polyploidy is a widespread condition of cultivated crops: more than two thirds of crop species are polyploids. This includes the *Brassica* crops, corn, wheat and many important cereals, potato, bananas, cotton, and sugarcane [22,23]. Allopolyploidy largely or entirely prevents recombination between alleles from the divergent parents, by turning the highly heterozygous chromosomes in the initial hybrid into homeologous chromosomes in the polyploid. This effectively preserves heterozygosity, with its potential for heterosis. This, and the doubling of genes available for evolutionary modification (including deletion), is thought to increase genomic plasticity, and thus fitness potential. Polyploids are also more tolerant to self-fertility which may favor a broader adaptive potential (i.e. ecological divergence) [23].

The ability to generate polyploids by artificial crosses and chromosomal manipulation using polyploidization agents gives access to early events following genome duplication, such as chromosome restructuring and loss of low-copy DNA sequences, activation of genes and retrotransposons, gene silencing, and subfunctionalization of duplicated genes [24]. Newly-formed "artificial" polyploids in *Brassica* crops and wheat undergo genome downsizing, rapid decay of synteny among homeologuous chromosomes and undergo epigenetic modifications [23] and refs therein) (also see Section 6.1). The non-random diploidization of (ancient) polyploids has been puzzling with regard to the classes of genes that are preferentially retained or lost. The most frequently retained gene/domain families are those encoding members of macromolecular complexes, such as the "enhanceosome machine", transcription factors and ribosomal components, and possibly members of large heterogenous families having wide spectra of functions, such as signal transduction gene networks [25–27]. The maintenance of critical gene networks is thought to be a buffer system against dosage sensitivity (stoichiometric effect) in macromolecular complex assembly.

Such capabilities could be further enhanced by mechanisms allowing polyploids to accelerate genetic change, as shown in *Arabidopsis* and maize ([28] and refs therein). In these species, the two sets of homeologous chromosomes are differentially altered, with modifications accumulating more readily in one set, therefore combining relative conservative and adaptive roles within the same nucleus.

2.3. Female reproductive fitness

Female reproductive fitness has historically been considered a major yield trait, with seed size and the number of seeds as the two quantitative trait components of female productivity in plants. Artificial selection and cropping constraints are expected to decrease the variability of seed size. A few large-effect QTLs are accounting for more than 20% of the variance in seed size in several crops [29] and refs therein). Seed number is a plastic trait responding more readily to changes in the availability of resources. A trade-off between seed number and seed size can occur depending on resources [30] (also see Section 6.3).

2.4. Yield enhancing genes

Such genes have been the focus of intensive research during the last 3 decades or so. Single genes for tiller number, dwarfing, and branching have been crucial in cereals [31]. Artificial selection in maize has affected 2–4% of maize genes, many being clustered near QTL loci for yield [32]. Among the first loci identified were alleles of *fruitweight2*, a major QTL for fruit size in tomato, and *teosinte branched1*, an inflorescence architecture and plant yield factor in maize [33]. These genes evolved as adaptations to domestication pressure. Over the past 25 years, one new gene with an established phenotypic effect on crops has been identified every year on average using forward genetic approaches. In comparison, limited reverse genetics approaches have already identified 50 genes in maize that have a domestication signature in the DNA sequence of adapted alleles. It remains to be understood whether most of these genes had an important historical adaptive role [34].

3. The current understanding of bioproductivity – hitting the yield ceiling

Bioproductivity is a key characteristic of biological resources. Productivity is essentially understood and evaluated as *production or yield* (see *supplemental files S1 and S2*, summarizing in glossary format the various terms in use). How much harvested biomass one can produce by growing a given genetic material or by a particular biological community in a given environment is what appear to matter most to farmers.

The Food and Agriculture Organization takes the following approach to gauge the *yield potential*: the average attainable yields for test-plots, crops, and technologies that are modelled to give yields obtainable under the same climate and technology on land without constraints on soil and terrain. This is termed the maximum constraint-free yield [35,36]. Ideal yields are much higher than realized yields in stressed environments, globally the most widespread in world agricultures. For example, cereal production on non-irrigated land would be roughly half of the *potential yield* (see Section 4) with irrigation [37], provided there is water availability at critical developmental stages [38,39].

Realized yields in agriculture (as assessed in field plots in different locations, etc.) have improved over time through the combined effects of fertilization, enhanced disease protection, adequate and timely weed control, better water availability and, last but not least, increased *genetic yield potential* (*Y*). The latter designates the yield "*a crop can attain under optimal management practices and in the absence of biotic and abiotic stresses*" and can be formalized by the equation of Monteith: $Y = 0.487 \cdot \mathrm{St} \cdot \varepsilon_i \cdot \varepsilon_c \cdot \varepsilon_p$ [40], where St is the duration of the growing season, ε_i, light interception efficiency, ε_c, photosynthesis efficiency, and ε_p, harvest index.

The increase in yield potential through conventional breeding over the past 50 years in maize, rice and wheat [7] resulted from the combined enhancement in harvest index and in light interception efficiency [40]. Increased harvest index has been achieved through dwarfing (shorter, more compact stem) and through improvement in seed set and in fruit and/or seed size. Increased light interception efficiency has required the development of larger-leafed cultivars and better arrangement of leaves. Dwarfing also contributed to enhance realized light interception efficiency by decreasing lodging.

Soybean cultivars from the United States of America have been bred with maximized ε_i and ε_p, and intercept almost 90% ($\varepsilon_i = 0.9$) of the photosynthetically active radiation, and allocate 60% of the biomass energy-equivalent to seeds ($\varepsilon_p = 0.60$). Thus, the yield traits in intensively bred varieties that drove the previous yield increases "*have little remaining potential for further increases*" [40].

Obviously, the "simple" methods to increase yield have already been applied. The prospects of further increasing yields seem to rely almost exclusively on increasing the length of the growing season (an environmental factor) and/or increasing the photosynthesis efficiency (a genetic factor) [40]. We argue that the early closure of canopy and the efficient use of photosynthates by the plant should also be considered (see Sections 5.1 and 6.2).

How real is such a limited range of future breeding options? To address this point, we first revisit the concept of bioproductivity in the light of integrated approaches and tools of plant science (Section 4); and second, we analyze the main general processes and mechanistic bases of bioproductivity at metabolic, genetic and developmental levels, in order to identify putative new levers or approaches for yield improvement (Sections 5 and 6).

4. Reframing bioproductivity—integrating the agro-ecosystem ceiling with systems level processes

Plant science is faced with a strong challenge: ensure yield security while shifting breeding goals in order to produce more with less. A global analysis of yield patterns using geospatial data has estimated that by optimizing worldwide *potential yields* (*as realized or attainable yields*) of major crops, i.e. by increasing agricultural resource efficiency, global food production could be increased by approximately 30–60% with current agricultural practices and technologies [10]. An OECD-FAO report (2012) states that agriculture production must increase by 60% over the next 40 years to satisfy the need for global food security in a world with a quarter of agricultural land being highly degraded and with increasing water scarcity [41]. Other experts estimate that the needed increase in crop yields is 120–170%, depending on demography, world grain stock strategies, and the evolution of current diets [42].

To understand how accurate such estimates could be, we need to achieve better thinking of what bioproductivity is, to decipher its foundations and to measure it at various organizational scales. Attention must be given to ways of achieving the optimized expression of a given productivity potential under environmental and human constraints by comparing conventional agriculture and alternative agricultural systems. The issue then becomes translating the yield ceiling into a more comprehensive agro-ecosystem ceiling.

Therefore, we investigate bioproductivity through the prism of Eco-Evo-Devo (Ecology and Evolution of Development). The quantity and/or quality of biomass rely on morphological and physiological diversification, innovations, and optimizations. These encompass adaptational mechanisms and processes that generate diversity at different organizational scales, from the metabolic/biochemical to the population and habitat levels. Understanding the evolutionary dynamics of mechanisms that control these features is a current focus in developmental genetics studies (in comparative gene expression and regulatory networks genomics, phylogenetic reconstructions, etc.). The biochemical aspect is too often neglected when dealing with this component of adaptive productivity. Secondary metabolites confer high plasticity in dynamic environments by acting as protective agents in biotic and abiotic stress responses [43]. As such, plant natural products are harvested and used as dyes, polymers, glues, oils, waxes, flavouring agents, and drugs.

In a given (agro)-ecosystemic context, bioproductivity reflects the *adaptive efficiency* (*supplemental file S2*) of underlying biological processes, many of which are discussed here through the angle of resource reallocation: photosynthesis and ribosome processing, growth rate control, plant architecture and light capture, energy and nutrient/water use. The range of phenotypic variation that a particular genotype is able to produce is defined as "its norm of reaction" [44]. The wider the reaction norm, the more plastic that genotype should be under changing selection conditions while retaining a narrow range of realized yield.

A theoretical *productivity potential* defining the best realizable outcome (biomass, for example) can be estimated by measuring the processes and mechanisms that contribute to yield under optimal growth conditions. One could then model how the best results achieved would translate into yield. The actual *expression of the potential* (termed "realized yield" in agriculture) under diverse environmental/climate conditions and cropping practices constraints (mainly soil, water, and inputs) is of particular interest as it measures various levels of adaptive capacity and plasticity (termed "performance") as a series of productivity numbers. Low input/high output agriculture is undoubtedly going to depend heavily on research encompassing everything from theoretical yield potential, biological efficiency, to realized yield over the long term and the corresponding environmental costs.

To that end, the impressive range of research tools generated in the last two decades (mainly systems biology and high-throughput methods) [45] will allow us to ultimately predict phenotype from genetic information and to predict ecological effectiveness from the phenotype. To reveal the (yet) hidden potential for the improvement/optimization of various agronomic traits, crop breeding methods cover now a broad spectrum of capacities: from the full understanding of genome architecture to the use of large-scale phenomics, and from rationalization, notably through the use of computerized field tracking, to the use of biometric methods in the assessment of interactions between genotype, environment, and management ([31] and refs therein; [46]). Last but not least, systems biology can ultimately be used to predict ecological effectiveness from the genotype. So far, many ecophysiological/organism models have been obtained, but only a few integrate the molecular level. Current research tends to integrate molecular models into ecophysiological models [47].

Finally, the metagenomics of communities will allow deep insights into adaptational strategies of diverse plants in many habitats. Eco-Evo-Devo studies will further dissect how domestication and breeding shaped the genomes, morphologies, and metabolic traits of species that underwent directed selection [48]. Here we focus on the intrinsic potential of plants to improve yield.

5. The biological foundation of plant productivity—three key general processes

Plant architecture is the result of two interrelated processes: the rates and patterns of organ formation at the apex, relative to the rates of growth of organs and internodes. Architecture is important for productivity in multiple ways, such as contribution to photosynthetic and water use efficiencies and to the ability of grain crops to avoid lodging. Plant growth is the direct expression of biomass production, driven by photosynthesis, which primarily depends on light, water, and nutrients. Below we consider these biological processes that determine the effectiveness of plant bioproductivity, bearing in mind that they operate as a continuum, as best illustrated with heterosis (see Section 6.1).

5.1. Photosynthesis

From light capture to carbohydrate synthesis [49], the maximum theoretical "conversion efficiency of solar energy to biomass is 4.6% for C3 photosynthesis at 30 °C and today's 380 ppm atmospheric CO_2, and 6% for C4 photosynthesis" [49]. This C4 advantage over C3 (at 30 °C) is expected to disappear if atmospheric CO_2 nears 700 ppm [40,49]. The observed maximal photosynthetic efficiency (ε_c), represents approximately one-third of the theoretical

maximum levels. For example, the efficiency of solar energy conversion into biomass under optimum growth conditions in sugar cane, a highly productive C4 crop, is approximately 2%, which corresponds to yields of biomass up to 150 tons/ha/year [50]. In other words, breeding for improving yields has made little, if any, progress in enhancing photosynthetic efficiency by itself.

Photosynthesis, including the Rubisco enzyme that fixes CO_2, evolved without the complication of molecular oxygen in the environment. This photosynthesis created our oxygen-rich atmosphere. Its history explains the unfortunate, insufficient selectivity of Rubisco to distinguish between CO_2 and O_2 in the carboxylation step of ribulose 1,5 diphosphate. At low, but not atypical levels of CO_2 in leaves of C3 plants, O_2 may be combined with the sugar instead of CO_2 [51]. Recovering from the addition of O_2 results in the release of a CO_2 molecule, termed photorespiration. This dramatically reduces photosynthetic efficiency [52], net losses of carbon being estimated at 25% [8,53].

The selectivity of Rubisco is temperature sensitive, becoming poorer at higher temperatures. The inefficiency of Rubisco is highlighted by its abundance: it is the most abundant protein on the planet, constituting up to 50% of the protein in the leaves of C3 plants. By contrast, C4 plants use a CO_2 concentrating mechanism, requiring ATP to increase CO_2 levels around Rubisco, which largely prevents photorespiration, allowing C4 plants to have higher photosynthetic efficiency and higher yields than C3 plants at high environmental temperatures [40,54,55]. Of note, maize, sorghum, sugar cane, and *Miscanthus* belong to the C4 subtype.

C4 plants also show higher water and nitrogen use efficiency than C3 plants [56] (see Section 6.4). Water use efficiency, the ratio of biomass produced to water used, can be improved by generating more biomass and/or by using less water. C4 plants can do both. The more efficient C4 photosynthesis directly increases biomass production. More interestingly, the concentrating mechanism of C4 plants is so powerful at pulling CO_2 out of the air spaces of the leaf that the CO_2 concentration in these airspaces becomes very low, so the difference in CO_2 concentration between the leaf and the atmosphere becomes larger. This increases the rate of diffusion of CO_2 into the leaf, so stomata can be made smaller or less numerous without impeding photosynthesis. This has the secondary effect of reducing water loss by transpiration. This can remain important, under water limitation, even as atmospheric CO_2 concentration increases. C4 plants have higher nitrogen use efficiency because they do not need to make so much rubisco protein as C3 plants [56,57].

A chloroplast photorespiratory bypass has been engineered into *Arabidopsis thaliana* that reduces the loss of fixed carbon and nitrogen occurring in C3 plants. This consisted in transforming the 5 gene-based glycolate catabolic pathway from *E. coli* into the plant nuclei. The result was an increased biomass production (measured by dry weight) and improved photosynthesis (measured by chlorophyll fluorescence) by an average factor of 1.5. The explanation was that the expression of the *E. coli* pathway enhanced the plastid CO_2 concentration [58].

Going further on these lines to enhance productivity through improvement in photosynthetic efficiency requires the proper understanding of an entire set of factors. Engineering and fine-tuning these factors are obviously a major challenge [8,40,49,53], requiring research on: (1) the negative feedback regulation of photosynthetic products and the regenerative capacity of the Calvin cycle; (2) the optimization of mineral nutrients availability and deployment to various parts of the plant and to cellular components in conjunction with circadian clock (see Section 6.1.2) and water transport controls; (3) the optimization of canopy architecture and chlorophyll content; (4) the reduction of photorespiration; (5) the rate of recovery from photoprotective states; (6) the engineering of Rubisco with increased carboxylation rates or with dramatically decreased oxygenase activity; (7) the convertion of C3 plants to a C4 type system.

C4 photosynthesis has evolved independently about 62 times in angiosperms [55]. There are several genera that include both C3 and C4 plants, and also include species that have intermediate features. The presence of this transition among relatively closely related species simplifies the elucidation of evolutionary mechanisms, because other evolutionary changes among these species are comparatively minor. Ongoing studies of these plants are revealing manifold changes in both the physiology and the morphology of leaves [59]. In spite of this complexity, there are now efforts to make C3 crop plants, such as rice, into C4 plants [53,60]. It remains possible that a *deus-ex-machina* could be found, using some simpler mechanism. Indeed, a bicarbonate transporter is known from cyanobacteria, and has been inserted into rice, and results in substantially increased photosynthesis, productivity, and yield (up to 70% in field trials) [53,61], and also higher efficiency in the use of water and nitrogen [56,62].

The question now becomes how such various enhancements in the laboratory will scale, in particular as it is difficult to reproduce the yield parameters of a whole growing season in such an environment [40].

Along such ideas, free-air CO_2 enrichment (FACE) experiments have been conducted for more than 20 years to expose open-air vegetation to elevated concentrations of atmospheric CO_2 [63,64]. The main results of these adaptive approach experiments demonstrated an increased net primary production and photosynthetic carbon gains, but also increased nitrogen- and water-use efficiency, and enhanced photoassimilate export to sink tissues. However, the increase in yield was much smaller than expected, with similar implications anticipated for natural systems [63,64]. Such a relaxation of photosynthesis (coined "photosynthesis aclimation") points towards the necessity to have a more holistic approach in achieving maximal benefit from increased atmospheric CO_2 [65].

Amongst alternative attempts, marine micro-algae domestication could significantly increase the photosynthetic primary production available to agriculture [66]. The first cost-effective systems might use marine algae cultured on seawater with added carbon dioxide from fossil fuels. In addition, micro-algae can be genetically engineered with value-added traits such as increased culture density, improved photosynthetic rates, improved amino acid composition, increased vitamin content or enhanced digestibility. Algae might (partly) replace feed grains such as soybean and also fishmeal and fish oil as used today in aquaculture [66]. The use of seawater in enclosed systems could allow algal-agriculture in coastal deserts. Strains of the fresh water alga *Chlorella pyrenoidosa* are already being grown commercially (in open ponds) as a health food (http://www.sunchlorellausa.com).

5.2. Ribosomes and protein complexity

Genome-wide screens in yeast indicate that ribosome biogenesis rates define cell size thresholds in conjunction with nutrient status [67]. Such screens have revealed further connections between cell size and translation in *Drosophila* (such as G1 phase translation regulators), not to mention a diversity of other cellular processes [68].

Ribosomes are central players for bioproductivity as translators of the genetic code into protein synthesis. Among the whole range of processes controlling the ribosomal machinery and the dosage of rRNA genes in plants and animals, methylation of cytosines at rDNA sites and chromatin modifications regulate rRNA gene expression [69]. For example, the developmentally controlled variation in their expression (nucleolar dominance) is highly sensitive to hybridization (see Section 2.1) [21]. Light, temperature, and

nutrient availability are environmental stimuli that affect such epigenetic switches [70–72].

Many mutations in ribosomal protein genes cause general growth defects and even lethality in *Arabidopsis*. Growth delay and defects can be observed at any stage of development. To fully perceive the major role played by the ribosomal machinery in biomass production, the phenotypes and likely reasons for the corresponding defects are summarized in Suppl. Table 1. Such phenotypes may reflect common trends towards a general reduction in protein synthesis, because defects in ribosome biogenesis affect ribosome number, which in turn perturbs a series of general functions, such as metabolism, cell proliferation, embryo formation, leaf size and polarity, plant size and biomass. Those defects also affect more specialized functions such as megagametophyte development, and thus grain yield.

The over-expression of ribosomal proteins or the increase of ribosomal biogenesis has occasionally been reported. For example, over-expressing ERBB-3 BINDING PROTEIN 1 (EBP1) in potato or *Arabidopsis* causes an increase of plant and leaf size [73]. EBP1 is part of ribonucleoprotein complexes in humans, thought to regulate the translational machinery in response to stress. The over-expression of the nucleolar C/EBPα in human cells leads to increased ribosomal biogenesis and cell size [74].

More systematic studies on the up-regulation of ribosomal proteins in plants need to be undertaken in order to design rRNA-based biotech strategies for increased yield potential. Such studies should also encompass the roles ribosomal proteins play in stress response in various crops. Some ribosomal proteins are specifically involved in biotic stimuli response. The RPL18, RPL24, and RPL13 proteins are targeted by a specific viral protein that is mediating the translation of Cauliflower mosaic virus proteins [75–77]. Therefore, specific modifications of ribosomal proteins could be a way to avoid or reduce unproductive interactions with proteins from pathogens.

It is obvious from this analysis that ribosome biogenesis and activity are key factors in understanding "bioproductivity potential" and the modulation of that potential, in particular in response to stress (also see Sections 4, 6.2 and 6.4).

Protein domain "shuffling" via genetic recombination leads to the emergence of particular domain combinations and domain refinement (via mutations, for example) that shape the functions of individual domains at the proteome level. They have played a major part in generating the great complexity of the eukaryotic proteome and led to functional innovations in multi-cellular organisms [78]. Seed storage proteins have immense effects on quantitative and qualitative aspects of bioproductivity, and domain recombination was likely a major source of their variations. Examples of such variations include the structural properties of the prolamins and globulins of cereals and their mechanisms of synthesis, trafficking, and deposition in the developing grain [79]. The diversity of wheat gluten proteins is crucial in determining the quality of the flour for bread/pasta/biscuit-making. Their domain composition and assortment has been diversely modified through breeding leading to changes in dough mixing properties.

5.3. Growth rate

Growth rate (*supplemental file S1*), together with metabolic rate, fertility, and life span are key life-history traits and describe life history strategies. While many species have plastic growth rates, some evolutionary patterns of interspecific variation in growth rate emerged [80]. Such patterns tie physiological properties (growth rate, RNA content, and cell size) and genome size [81], also see [68]). In particular, genome size and RNA concentrations are usually negatively correlated, while RNA content is usually positively correlated with maximum growth rate (also see Section 5.2) [81]. Weeds, which have high growth rates, typically have small genome sizes [82]. This suggests that, at least in some taxa, reduced genome size (called "genome streamlining") could be a consequence of a selective pressure for high growth rate, one major adaptive strategy during evolution.

Selection for improved growth rate was, and remains, one major target of domestication, breeding, and agricultural practices (also see Sections 6.1 and 6.2). For example, nutrient limitation or nutrient excess (P demands for RNA and DNA, N demands for proteins)–i.e. the extremes of daily agriculture–may have impacted on life-cycle processes, genome/cell size, and division rates of various crop species (also see Section 6.4). Obviously, more systematic studies on these lines are needed (for example on polyploid crops; see Section 2) to further our understanding on how agricultural sciences have channelled the yield/productivity potential of various crop species.

6. Mechanistic bases of productivity: key examples

The chosen examples illustrate processes controlling productivity and yield at the levels of the entire organism, the individual organ, and the cell. They also help in understanding what we termed "productivity potential" and the factors that modify its expression (i.e. the realized yield/performance; see Section 4).

A few master ("magic") genes have been identified as major players in plant productivity, most famously those involved in domestication [18] and those for dwarfing, that were at the heart of the Green Revolution [31]. More recently, genes that control developmental phase transitions have been found [83], which act as rheostat genes, triggering large-scale shifts in gene expression involving vegetative and reproductive traits. These are discussed below.

6.1. Heterosis

"*Heterosis is the phenotypic superiority of a hybrid over its parents in growth rate, reproductive success, and yield*" [20]. Several other terms for heterosis are in use, including hybrid vigour, growth vigour, morphological vigour, hybrid performance, superior performance, and agronomic performance. The most appropriate scientific terms should be "heterosis" and "hybrid vigour", but it might be helpful to specify different terms for intra- versus interspecific heterosis, in particular if the main mechanistic bases are rather different between the two categories. The opposite effect, termed "inbreeding depression," or "vigor breakdown" is also known, but is ignored most of the time.

6.1.1. Intraspecific heterosis

Intraspecific heterosis is the phenomenon whereby the progeny from crossing particular inbred lines of the same species have enhanced agronomic performance relative to both parental lines as well as most open pollinated varieties. To that end, parental inbreds produced through successive selfing generations are tested for the productivity of their F_1 hybrids (after crossing with other inbred lines).

Heterosis has contributed to increase yields starting with the introduction of "F_1 hybrids" of maize in the 1920s. Yield advantages in maize, sorghum, rice, or sunflower have ranged between 15 and 50% [84]. F_1 hybrids have additional technological advantages: their morphological uniformity and increased response to fertilizers. Therefore the debate on yield potential in open-pollinated vs hybrid varieties goes far beyond the biological process per se.

Phenotypic traits and interactions that exemplify the benefits of heterosis. Heterotic phenotypes concentrate on total grain yield, but also include "*seedling biomass, plant height*, [. . .] *the rate of*

vegetative growth, flowering time, inflorescence number, flowers per inflorescence, fruit or grain set, and fruit or grain weight" [20].

Interestingly, such interactions can be affected by environmental factors, since grain yield in F_1 hybrids were superior to their parental inbred lines when grown under drought conditions and at greater plant density. Such differences in yield were explained by differences in plant water-use traits (mineral accumulation, relative water content, lower leaf temperature, stomatal conductance and steady-state chlorophyll fluorescence), implying improved water use in F_1 hybrids [85] and ref therein).

Genetic and molecular bases. The heterozygous advantage provided by heterosis is a buffer against deleterious recessive alleles and represents a source of genetic plasticity under changing and variable environments [20]. Heterosis is affected by gene dosage and allele composition [86] and is correlated with epigenetic profiles showing rapid and extensive changes in small RNA gene expression and distribution in hybrids as compared with their progenitors [87]. Such small RNAs play a buffering role in genomes newly combined through hybridization/polyploidization [88].

There has long been a dispute whether heterosis results from heterozygosity at particular loci between the alleles from the two parents (i.e. the nonadditive situation), or whether the combination of interacting alleles at different tightly linked loci achieves heterosis (i.e. the cumulative effects of gene interactions) [89]. In either event, if heterozygosity per se confers heterosis, the phenomenon should break down due to recombination [20]. If alleles of individual genes confer beneficial phenotypic effects through overdominance, they could persist in populations through heterozygote advantage.

The controversy remains due to the following observations: (1) gene interactions including additivity, high and low-parental dominance, underdominance, and overdominance have been observed when analysing heterosis [90]; (2) heterosis is influenced by environmental cues that blur the relative contribution of each of these mechanisms. However, dominance complementation, epistasis (i.e., gene interaction), and overdominance (synergistic interactions generating enhanced phenotypes) are the primary contributors to heterosis as they are preferentially selected through breeding [90]; (3) QTLs known to affect hybrid vigour have some degree of semi-dominance [91]; (4) polymorphism types have many presence-absence variants that contain intact, expressed, single copy genes that are present in one inbred line but not in others [22] and refs therein); and (5) global gene expression profiling using microarrays proved less informative on the molecular bases of heterosis than hoped, mainly because this type of analysis cannot incorporate the phenotypic effects resulting from multiple gene interactions acting together during development [20].

Breeding schemes can benefit from genome-wide information, such as dense genetic markers. They can be used to understand the state and the consequences of genetic variability across the genome in order to estimate, with higher accuracy, possible genetic gains and rates of (local vs. global) inbreeding. As such, the latter can help predict breeding values of candidates to selection [86].

Finally, there are examples of single "magic" genes identified as responsible for heterosis effects (termed "heterotic genes") [20]. Such genes could operate by rewiring regulatory hierarchies that control quantitative traits. Heterozygosity for loss-of-function alleles of a flowering time gene (*SFT*) in tomato strongly increased yield (up to 60%). The heterosis effect occurred in several genetic backgrounds and under diverse growth conditions. The mutation acted pleiotropically suppressing growth termination at the meristem(s) allowing indeterminate growth. Similar effects were observed by over-expressing a specific micro-RNA, whose putative targets were meristem and flowering-transition key regulators [89,92].

In conclusion, heterosis is a genome-wide phenomenon resulting in increased organ size and robust stature, primarily through increased cell number [93]. A slight but continuous increase in hybrid vigour has been a main trend in breeding work over time. Selecting the best combinations of alleles has produced multiplicative/synergistic positive effects resulting in increased yield [91]. Because only a limited number of genetic interactions has been tested so far, high-resolution QTL mapping and genome-wide epigenetic profiling need to be combined with "phenomics" platform capacities, to measure multiple traits at the same time in large population samples. The selected phenotypes will facilitate the QTL-cloning of an increasing number of heterotic genes.

6.1.2. Interspecific heterosis

Interspecific heterosis is the phenomenon whereby F_1 hybrids, segregating hybrids, and stable allopolyploids derived from interspecific crosses have enhanced agronomic performance relative to both parents [94]. Allopolyploids such as wheat, triticale, oilseed-rape, and tobacco are classical examples, but we concentrate on a couple of recent synthetic allopolyploids designed to analyse the genetic and molecular bases of heterosis.

Genetic and molecular bases. *Arabidopsis* allotetraploids are larger and grow more vigorously than the *Arabidopsis thaliana* and *A. arenosa* parents [94]. The epigenetic modifications of the circadian clock genes of the hybrids and allopolyploids mediated changes in the amplitude of gene expression in downstream genes involved in energy and metabolism, including chlorophyll synthesis and starch pathways. The results suggested that the advantages gained from the novel genomic interactions and leading to altered control (resetting) of circadian clock-mediated processes resulted in increased biomass (also see Section 5.1). These findings are in agreement with observations that the circadian clock alters metabolic pathways in ways that inhance fitness in both animals and plants [95].

Interspecific hybrids between *Antirrhynum majus* and closely related *Antirrhynum* species were generated and flower shape and colour, and leaf shape and size were evaluated [95]. In such closely related species, quantitative variations in the chosen traits were either small or "cryptic" (i.e. no phenotypic effects were detected). Interestingly, extensive inter-specific differences were observed when studying gene expression patterns in the hybrids and parental lines. The study compared the extent of variation in gene expression and that of change in phenotype at chosen interacting loci. The observed differences indicated that the range of expression variation for specific genes was less constrained in hybrids than in the parental lines. Such differences related to small quantitative effects in the corresponding phenotypic traits. The authors concluded that individual loci with small variation effects can synergistically combine their effects and result in either hybrid superiority or inferiority [95].

In conclusion, the analysis of *inter- and intra-specific heterosis* indicates that the hybrid performance and fitness relies on newly acquired capacities that boost interconnected basic cellular processes due to genome-wide (epigenetic) relaxation of gene expression and interactions (pleiotropic heterotic mechanisms). Hybridization and polyploidy (see Section 2) offer permissive genomic contexts for heterosis. It is very likely that domestication and breeding have systematically shifted the equilibrium towards superior performance through selection for modified compensatory tradeoffs for yield traits.

6.2. Plant geometry: the contribution of plant architecture and organ size

Plant biomass production is controlled by a series of factors, the most critical being plant architecture and organ size. Plant organs

evolved as independent assortments of structural/functional units that greatly facilitate the selection of desired yield traits. We concentrate on the approaches that help us understand the contribution of master gene regulators and herein reviewed processes (Section 5) to plant productivity.

6.2.1. The modularity of plant architecture—from meristems to cell walls

Most plants have body plans of indeterminate, iterative growth, which provides the capacity to respond in an elaborate and robust manner to environmental signals [96]. Specialized growth niches have been separated and spaced out during evolution: angiosperms (and thus crop species) exhibit discrete zones with the potential for rapid cell proliferation (i.e. meristems) versus specialized and high metabolic activity (i.e. organs such as leaves). The aerial architecture of plants results from the concerted associations of modules, called phytomers, which comprise an organ, an internode and a meristem. How the sequence of these modules is arranged provides great plasticity, allowing the plant to adapt to a changing environment [97]. A large diversity of architectures can actually be observed in nature [97] and a continuum between these architectures can even be generated in silico, using a small set of parameters, relying on the modular architecture of plants [98]. This suggests that plants can in principle produce any type of architecture.

The gene networks that regulate meristem activities have been the focus of intensive research during the last two decades [99–103]. Interestingly, these genes have been isolated in mutant screens using criteria that were, in essence, similar to crop selection and crop improvement during domestication: in the laboratory, the most promising mutants for meristem functions were the ones with altered flowering time followed by those with increased or decreased organ number. A large set of master regulators, most of them transcription factors, was obtained, with several candidates having a potentially important role in yield optimization [104] (see also [105] for a case study in wheat).

For instance, the KNOX proteins are homeodomain transcription factors that maintain pluripotent cell populations at the shoot apical meristem and elsewhere in the plant. They control hormone homeostasis in the meristem, [106]. KNOX proteins are well conserved and control the diploid, sporophytic development of all major lineages of vascular plants [107]. Because they are required for meristem maintenance, and by extension plant productivity and adaptability, *KNOX* genes can be considered as developmental timekeepers by controlling biomass maturation schedules [108]. Branching, a classical trait that has been repeatedly selected for, also depends on meristem activity. For example, *teosinte branched 1* (*tb1*), a TCP transcription factor, has been altered during maize domestication resulting in plants with fewer or no tillers, concentrating resources in the main stem, as well as additional changes in female inflorescence formation [33]. More generally, apical meristem activity has been a major target of plant domestication/breeding: varieties adapted to more uniform ripening, mechanical picking, or short season cropping have determinate and partial-indeterminate apical meristem growth.

In the past decade, the genetic basis of meristem biology has been further integrated with hormone signalling, thus providing mechanisms through which the plant can modulate its architecture in response to its physiological state and/or environmental cues. For instance, KNOX proteins have been shown to increase cytokinin levels, while being repressed by gibberellins [106]. The corresponding perception and transduction hormonal pathways have been identified in the past two decades [109–114], and almost all hormone-response signal transduction pathways interact with each other during all stages of plant growth and development [106]. As these interactions also include multiple feedback loops, this renders any predicted output from hormonal inputs rather difficult. This also explains the current shift in computer simulation strategies to make such predictions [115,116].

While this accumulation of data provides a number of convenient levers with which to modulate plant architecture, this is not sufficient to causally link gene activity and plant shape (and thus to make credible predictions for plant yield). It is only by taking into account the impact of these regulators on the mechanical properties of cells that one is able to understand how genes control shape changes. As the biophysics of plant cells mainly resides in the cell wall, this is where the new frontier in plant development is. Not surprisingly, the link between master regulators of development and the cell wall is also attracting attention for the control of plant biomass [117,118].

Large families of cell wall regulators have been identified and mutant screens often based on hypocotyl elongation defects in *Arabidopsis* has provided a number of important actors in primary cell wall synthesis, such as cellulose synthases [119]. Secondary cell wall formation is actually an important component for biomass because the bulk of plant (dried) biomass consists of vessel elements and fibers (with cellulose, xylans, and pectins as major constituents). This is also under hormonal control. For example, altering gibberelin biosynthesis and signalling by overexpression of a GA20-oxidase in poplar resulted in a doubling of stem dry weight as a consequence of increased plant height and fiber length [118]. In general, increasing synthesis and signalling and decreasing catabolism of GAs and brassinosteroids is expected to produce taller phenotypes. Optimising plant architecture for biomass nowadays exploits integrated QTL mapping and gene networking, as well as mutant and phytohormone analyses [120]. Transcriptomics associated with mutant analysis in Arabidopsis has tremendously increased the number of putative regulators of secondary cell wall formation in recent years [121]. Furthermore, new methods are currently developed to explore the ultrastructure of plant cell walls, like atomic force microscopy or synchrotron radiation microdiffraction [122], and these should provide essential clues to better understand how the mechanical properties of cell walls, and thus their extensibility, can be modulated.

6.2.2. The regulation of organ size

In addition to the modularity of plant architecture, organ size control is a central component of plant productivity. Beyond the basic growth-regulating processes of cell cycle control, cell elongation and ribosome biogenesis, progress has been rather slow in understanding how organ initiation and growth is controlled, resulting from the combined effects of spatially coordinated growth rates and tissue polarities [68,96]. Organ primordia undergo differential cell division programs patterns followed by post-mitotic cell expansion, accompanied by ploidy increase (endo-reduplication) and cell wall remodelling [123]. Many actors involved in leaf growth have been identified and highlight the main checkpoints behind the final size of leaves. These include the size of the shoot meristem (e.g. CLV3, cytokinin), number of cells recruited in the primordium (e.g. SWP), proliferation rate (e.g. APC10, SCF) and transition towards cell expansion (e.g. ANT, TCP4, miR319) [123]. Among the identified factors, a few also promote cell differentiation/expansion (TCP factors, auxin signalling, ribosome biogenesis) that link cell growth to the availability of metabolic resources [68,96]. Interestingly, as observed for plant architecture, the final size is itself a flexible outcome: both in monocots and dicots, the base of the leaf maintains a meristematic potential, which may fine-tune the final organ size.

The final organ size is actually the result of many intertwined processes, and this complexity sometimes leads to counterintuitive results. For instance in the *ant* mutant, while cell number is reduced, organ size is not dramatically impacted, as leaves exhibit increased cell size [123]. These so-called compensations are extremely

frequent and illustrate how the interconnection between pathways leads to robustness in organ size. This also suggests that a clear understanding of the interplays between the pathways is crucial to identifying the major modulators of organ size. For instance, EBP1 has been shown to promote both cell division and cell expansion. As the impact on cell division is limited to non-differentiated cells, gain of function EBP1 plants do indeed exhibit organs with increased size [123].

An additional dimension concerns fruit size and quality. Assimilate partitioning to the fruit is a major component of yield. The tomato QTL (Brix9-2-5) is an apoplastic invertase that modulates sugar partitioning to the fruit and has been used to increase total soluble solids, sugars in particular [124]. With this and many other genes identified in the last decade, fruit size and quality is beginning to be understood in terms of source-sink relationship (carbon and amino nitrogen ratio, glucose signalling, the rate of export and hydraulic conductance properties of the phloem, plasmodesmata conductace, complementary roles of auxin and GAs and cross-talk with sugar signalling) [125].

Confronted with such complexities, strategies inspired by synthetic biology are being used to simplify the gene network in silico and reduce it to a small set of factors that would be sufficient to have a major impact on the agronomic potential of crops, like tomato [126]. While these strategies are still in their infancy, there is no doubt that novel tools, such as "computational genome redesign", will become more widespread and help identify the most promising pathways to modulate plant productivity.

Another layer of complexity comes from the fact that the final organ shape can in turn act as an instructing signal on the genetic network. The interactions between the macroscopic level and the local effectors are attracting increasing attention in basic research, and often involve modeling strategies. This multiscale approach is likely to become more widespread in crop science too, and this may thus shift the focus from molecular biology towards new modeling approaches that integrate the dynamics and topology of gene networks with their macroscopic outputs [116]. Organ size seems to strongly depend on the timing of the arrest of cell proliferation. Changes in cell number and the modulation in the duration of the cell proliferation phase have been associated with two transcription factor/micro-RNA – based genetic pathways [68,96]. Among the identified factors, a few also promote cell differentiation/expansion (TCP factors, auxin signalling, ribosome biogenesis) that link cell growth to the availability of metabolic resources For instance, although it is crucial to determine organ size, how growth arrest occurs remains an open question. It has been proposed that, as an organ increases in size, the concentration of its principal morphogen may become diluted, thus triggering growth arrest and determining the final size of the organ in a feedback loop [127]. An alternative model has been proposed: as the organ increases its size, internal tissues become more compressed and this may lead to mitotic arrest [128]. These different scenarios illustrate how geometrical or mechanical feedbacks may add robustness to the final shape of organs.

Mechanical cues may in fact have a more widespread role in the control of organ size than generally thought. It is well known that wind makes plants shorter and stiffer, demonstrating that plant tissues are able to sense, and respond to, their mechanical environment. This is also true at the cellular scale: the expression profile of many genes is affected when plants are bent, and it is believed that the so-called *TOUCH* genes represent at least 2.5% of the genome [129]. While the mechanoperception pathway has remained elusive so far, there is accumulating evidence showing that major regulators of plant growth are under mechanical control. For instance, mechanical stress controls cortical microtubules orientation, which controls anisotropic growth via the oriented deposition of cellulose. This changes the cell wall properties and thus organ shape [130,131]. The subcellular localization of the auxin transporter PIN1 has also been shown to depend on membrane tension, thus providing a mechanism relating pattern of mechanical stress to auxin fluxes in tissues and plant architecture [132,133]. As mechanical forces cannot be visualized, this research heavily relies on mechanical models and computer simulations.

In conclusion, the manipulation of organ growth and plant geometry is a strategic ag-biotech target for enhancing the productivity potential of crops, or alternatively, for facilitating harvesting and processing activities. Breakthroughs in the next decade may come mainly from systems biology. Modelling may translate the biological puzzle described above into an emergent picture of organ growth patterning as a virtual root, petal, fruit, seed or tree. This also relies on our ability to generate and organize databases compiling all the main growth regulators and their interactions. This is already underway: a systematic approach termed the "Yield booster" program (www.yieldbooster.org/about-us) is being used to study genes and mechanisms governing plant growth and productivity. Functional genomics, gene expression profiling, interactomics, metabolomics, and large-scale phenotyping are employed to explore cell cycle, endoreduplication, cell polarity and trafficking, hormone signalling and cross-talk, and leaf and biomass formation. This approach provides gene regulatory network maps, integrating the current knowledge on transcription factors and their role in development [134] and an open list of "intrinsic yield genes" and phenotypes resulting from the miss-expression (overexpression and loss-of-function) of genes known to affect plant growth and development [135].

Among single "magic" regulatory genes, biomass enhancement has been associated with alterations in developmental timing (phase transition) genes in *Arabidopsis*. A highly conserved component of histone deacetylation complexes, FVE/MSI4, has been associated with accelerating developmental transitions during ontogenesis [99]. Fast cycling results in low biomass production in the wild type. The genome is largely reprogrammed in the corresponding mutant, leading to pleiotropic, environmental-dependent effects on plant architecture. For example, depending on the photoperiod, the vegetative biomass in the mutants is increased 3 to 8-fold due to enhanced leaf, fruit, and seed size and number. The main functions of the gene are to control the organ initiation rates at the apical meristem and the balance between cell proliferation and differentiation in the leaves. Mutant and overexpressor lines had no morphological aberrations. Genes of this kind are ideal for engineering biomass according to geographical or climate constraints [99].

6.3. The rice yield system

The rice model reviewed below summarizes known yield-enhancing processes in a major crop. After the 1950s, rice yields doubled in most parts of the world. Today, yields are leveling off. For example, "*between 1987 and 1997 China increased its average rice yields from 5.4 t/ha to 6.4 t/ha*". Since 1997 rice yields remained at that stable level [40] and http://www.foodsecurityportal.org/api/countries/fao-production-rice).

Three genetic improvements contributed to rice yield increases: improved harvest index (see Section 3), adapted plant architecture, and exploitation of hybrids [23]. Agronomically, the grain yield of rice is the combined outcome of three constituents [136]:

(1) The sink system, is a complex trait associating number of panicles, number of grains per panicle, and grain weight. Impressive achievements have been obtained in sink capacity and will be detailed below.

(2) The source system provides carbohydrates to the sink via photosynthesis. The genetic variation in the rice germplasm should be further explored for traits affecting plant architecture and canopy development, the ability to maintain green leaves, and improved photosynthetic rates to increase photosynthetic efficiency under different environmental conditions (see Section 5.1).
(3) The flow system transports the photosynthate products and other nutrients through the vascular system and via a series of transporters into the sink. As with the source system, the very first step for improving the transport capacity should be to systematically exploit the existing genetic variation for translocation capacities from the source to the sink.

The dissection of the genetic bases of sink yield traits [136] is summarized below.

6.3.1. The number of panicles

The number of panicles is dependent on the tillering ability (or shoot branching capacity) and may include several high-order tillers. The trend is to breed for enhanced apical dominance, i.e. for fewer and larger panicles, because grain yield usually results from the primary and some early secondary tillers. The rice genes controlling axillary bud activity and the branching signalling pathway [137] are conserved between monocots and dicots. These genetic mechanisms underlie the contrasting roles of auxin and cytokinins, along with signalling through strigolactones. Quantitative differences in tiller numbers are also influenced by environmental factors, such as planting density and fertilizer level.

6.3.2. The number of grains per panicle

The number of grains per panicle depends on two main factors: the number of spikelets and seed setting rates of the spikelets. Panicle architecture results from a complex sequence of the initiation and maintenance of axilary meristems of high-order panicle branches. For example, spikelet number per panicle can vary from 60 to more than 500. Selection for increased panicle size has revealed the involvement of shared meristem regulators for both tillers and panicles. Cytokinins regulate the rate of spikelet formation, and conserved gene networks control panicle initiation and differentiation, influenced by photoperiod, circadian rhythm, and light signalling. Light signalling, for example, controls the balance of floret formation and spikelet axillary branching through conserved genes of the *TERMINAL FLOWER*, *LEAFY* and *CONSTANS* families [138,139].

These two yield factors control rice plant architecture and illustrate the highly-ordered system of branching and meristem transition to flowering, from tillers to panicles and flowers. Such traits also vary as a function of planting density, shading effects, fertilizer content and light/phytochrome regimes.

6.3.3. Grain weight

Comparison of small- and large-grain genotypes has shown that grain development is a spatio-temporal process of cell divisions, both longitudinally and latitudinally, and of grain filling. The few genes that have been characterized so far indicate that regulating cell division requires ubiquitin-proteasome processes, while grain filling is under the control of cell-wall invertases involved in carbon partitioning [136].

What are the ongoing efforts to increase the yield potential of rice? Dissection of the genetic bases of yield traits in rice focuses on two main yield potential traits: plant/panicle architecture (tiller number, panicle branching morphology, and stem vasculature structure) and grain properties (seed number and size) [140]. Ongoing research is taking advantage of the entire set of genetic and genomic tools generated for rice (such as insertion mutants, the vast numbers of polymorphisms and molecular makers, as well as specifically-designed mapping populations and detailed linkage maps that have allowed resolution of hundreds of yield QTLs [22].

On these lines, the transcriptome analyses of superhybrid rice has shown that (1) the identified differentially expressed genes confirm previously reported functional gene categories related to heterosis (see Section 6.1) and (2) map positions of several candidate genes correlate with yield-related QTLs [141]. The cloning and characterization of one such QTL with pleiotropic effects on yield traits–a "magic" gene – has been named IPA1, for Ideal Plant Architecture [142].

Finally, a breeding strategy aimed at achieving higher rice production and grain quality has been described as the "Green Super Rice" initiative [143]. The strategy consists in germplasm and mutant collection screening and gene discovery and functional analysis for biotic and abiotic stress responses and nurtient-use efficiency. Genes isolated for an increasing set of traits are systematically being incorporated into elite cultivars [143]. The associated IRRI project plans to develop "*at least fifteen new rice varieties and deliver them to small-hold farmers in Africa* (*seven countries*) *and Asia* (*eight countries including China*)" for a total of eleven million hectares during the next 3 years [144].

6.4. The genetic dissection of adaptive responses to abiotic stresses

The science of the Green Revolution focused on improving productivity by providing optimal cropping environments for high yielding genotypes designed to respond to such environments [145]. Today, the shifting of breeding goals towards a "low input, high output" agriculture [146] raises another key issue in the bioproductivity research area: the genetic dissection of quantitative traits controlling adaptive response and performance of crops under environmentally constrained conditions. We need to find QTLs for abiotic stress tolerance to drought (the most complex and devastating stress in crops), salinity, submergence and anoxia, extreme temperatures, mineral toxicities and nutrient deficiencies (i.e. nitrogen and phosphorus use efficiency). The effects of stress on productivity are most severe at certain developmental stages, such as male gametophyte development, the transition to flowering phase, or grain filling [147–149]. Studies on stress responses are now integrating primarily transcriptome, proteome, and metabolome profiling.

6.4.1. Drought: from tolerance to biomass optimization strategies

Improving yield potential and resistance to drought requires an understanding of the physiological basis of crop yield and its response to water deficit. "Drought tolerance" in xerophytes adapted to water shortages operates through water storage and/or conservation mechanisms. In other species, drought mobilizes an initial stress response, likely mediating a transient drought tolerance. Subsequently, stress (in)tolerance arises based on species- and variety-specific water use efficiency. Transient drought tolerance is basically oxidative stress tolerance. Reactive oxygen species function as signalling molecules controlling abiotic stress responses, but also programmed cell death, pathogen defence, and systemic signalling [150]. Better water use efficiency results in getting more grain per input water.

Photosynthesis and transpiration rates are inherently linked, as determined by leaf area and stomatal density and aperture in wheat, barley, and rice [151]. Other factors and considerations have been made in Section 5.1. Leaf growth rates decline rapidly under water deficit, and so does the production of biomass. Therefore, reducing such losses is a matter of optimizing the interactions among transpiration, biomass accumulation, and biomass partitioning, i.e. resource reallocation.

On these bases, three strategies aiming at reducing the risk of total yield loss due to water deficit are being developed: (1) the exploitation of natural variation for drought-related traits is producing tangible progress in securing yields [152]; (2) reducing total transpiration (by reducing the duration of the crop cycle, leaf area, or stomatal conductance) requires carefully designed experiments, as diminished yields or yield penalties could occur under mild or in the absence of water stress respectively [153,154]; (3) genetic engineering for dehydration tolerance with very promising results under laboratory conditions [153,154]. DroughtGard maize is becoming an ideal study case (see below) in efforts to transpose laboratory tests to field trials.

Finally, in a proteomics approach to study drought tolerance, quantitative changes were measured in protein abundance of wheat cultivars differing in their yield under drought [155]. Out of 1300 proteins identified, 159 changed in relative abundance in drought tolerant cultivars. The main changes involved oxidative stress metabolism and the reactive oxygen species scavenging capacity [155].

6.4.2. Nitrogen use efficiency

Changing "N economy" today through improved nitrogen use efficiency (NUE) by crops has been recognized as an urgent target for the Second Green Revolution. Up to half of the N added to crops is lost to the environment [156].

Soil nitrate concentrations fluctuate by an impressive 4-fold factor [157]. Nitrate uptake is tightly controlled by a series of channels in the plant [156]: nitrate proton-coupled transporters (60 genes in *Arabidopsis*), chloride channels and other anion and anion-proton exchangers. NUE starts with N uptake, but further requires identified genes from several pathways: assimilation, amino acid biosynthesis, C/N storage and metabolism, signalling and regulation of N metabolism and translocation, and remobilization/senescence. It is obvious that the links to photosynthesis, C/N signalling and plant architecture, changes in source to sink concentrations, and other factors including water availability are making NUE engineering a hardly predictable task. As a matter of fact, the manipulation of candidate NUE genes (nitrate uptake genes, glutamate synthase or glutamine oxoglutarate aminotransferase, (GOGAT) was unproductive. The overexpression in canola of alanine aminotransferase (with known roles in hypoxic/drought stress, C4 photosynthesis, N storage) maintained yields at control levels with 40% less N fertilizer application [157].

Along the classical breeding side, QTLs for NUE and maize grain yield components (such as ear number) were identified in responsive genotypes which, under low N, accumulated nitrogen (possibly in the form of urea) in the leaves and efficiently translocated the stored nitrogen from the source to the sink during the grain filling stage [154]. The identified genes encode glutamine synthetase, sucrose-phosphate synthase, sucrose synthase, and invertase (β-fructofuranosidase).

Finally, TraitMillTM – developed by CropDesign – is a high throughput platform annually analysing thousands of transgenic rice plants transformed with a large spectrum of candidate genes. The plants are grown in highly automated greenhouse under a diverse range of cultivation conditions [158]. The objective is to select genes that potentially improve seed yield, biomass production, and abiotic stress responses, in particular water- and nitrogen-use efficiency [158].

6.4.3. Substantial cross-talk and multilayer controls in stress-response processes

This section concentrates on the transcriptome, micro-RNAs, and the corresponding promoter elements to show the extent at which stresses and diverse physiological processes including nutrient deficiency operate in concert at this level of organization ([159] and refs therein). Of special note is work on poplar [160], exploring transcriptome profiles of the cambial region in water deficit versus re-watering conditions.

Transcriptome analyses of *Arabidopsis* and rice showed significant cross-talk between drought-, high salinity-, and ABA-response pathways [161]. The identified drought-inducible genes belong to two groups:

(1) Abiotic stress tolerance proteins, including protection factors, comprise "chaperones, late embryogenesis abundant (LEA) proteins, osmotin, osmolyte biosynthesis enzymes, antifreeze proteins, water channel proteins, sugar and proline transporters, detoxification enzymes, and proteases" [161,162].
(2) Regulatory proteins, including "transcription factors, protein kinases, calmodulin-binding proteins, protein phosphatases, phospholipid metabolism enzymes, and ABA biosynthesis" [161]. At least six signal transduction pathways operate in drought, high salinity, and cold-stress responses that protect the plant from reactive oxygen species toxicity and osmotic stress. The pathways act through families of transcription factors such as NAC, AP2, NF-YB, MYC, MYB, b-ZIP, HD-ZIP and are coupled to biotic and wound-response signalling via jasmonate signalling [161,162].

Micro-RNA profiling in rice at tillering and inflorescence-forming stages identified target genes and pathways of thirty drought stress-regulated micro-RNA gene families [159]. They include, in addition to a large set of cDNAs of unknown function: (1) various transcription factor families that have roles in stress responses (such as MYB, bZIP, zinc finger, CBF, HAP2, SBP, ACP1); and (2) genes involved in sulphur metabolism and ubiquinone biosynthesis, in starch and sucrose metabolism, and in CO_2 fixation. This implies that controlling the "*rate of synthesis of carbon–hydrogen compounds helps enhance stress tolerance under drought conditions*" (144).

The promoters of drought-, high salinity-, and cold-inducible genes, including microRNA genes, contain shared ABA- or gibberellin-responsive, anoxic-specific, and drought/dehydration-responsive cis-acting elements [159,161]. Stress-inducible promoters in rice had low basal levels of expression under normal growth conditions. Expression was increased up to 65-fold in leaves and ~1400-fold in flowers after exposure to drought conditions [163].

Many of these genes and promoters are now being tested by transgenic approaches. Transgenic crop plants that overexpress stress-induced transcription factors (such as AP2/ERF, NAC and zinc finger proteins) have greater tolerance to drought stress [163]. By including stress-inducible or organ-specific promoters to limit the expression of drought-responsive transgenes to times of drought stress, it is anticipated that a more discriminate response to drought can be achieved, without affecting productivity under water sufficiency.

Proteomic approaches study now the proteome reprogramming under conditions of environmental stress and report protein post-translational modifications and priming by eliciting factors (such as NO, H_2O_2, H_2S, or beta-aminobutyric acid) which resembles the systemic acquired resistance elicited against biotic stresses [164]. Stress warning systems are being explored by analyzing protein phosphorylation signalling pathways as an early manifestation of biotic and abiotic stress effects, in the so-called phosphoproteomics approach [165]. Emerging models stress the need to concentrate further studies on the stress signalling networks, and in particular on the MAPK cascades and modules [162].

Are there "magic" regulatory genes that alone can mitigate important levels of stress? *Arabidopsis eskimo1* mutant lines have increased tolerance to freezing, and are more tolerant to mild drought stress and to salt stress, indicating that the mutated gene has an important role in oxidative stress tolerance and water use

efficiency [166]. The gene encodes a plant specific protein whose malfunction primarily affects xylem cell wall composition, possibly at the esterification stage of pectin polymers, and modifies water transport through the xylem [167]. Transgenic maize plants with increased expression of a nuclear factor Y component are tolerant to drought, as assessed by several stress-related parameters (such as chlorophyll content, stomatal conductance, leaf temperature, reduced wilting, and photosynthesis rate) and by yield performance under water-limited conditions [168]. Furthermore, expression of the *Bacillus subtilis csp*B gene (encoding a cold shock protein B acting as an RNA chaperone) in *Arabidopsis*, rice, and maize promoted stress tolerance to cold, heat, and water deficits [149]. DroughtGardTM maize was obtained through the introgression of the *cspB* transgenic trait into conventional maize varieties [169]. The trait enhances the capacity of plants to withstand drought stresses, in particular when exposed at the critical pre-anthesis stages. The observed lower yield losses in these plants, compared to controls, likely resulted from an improved use of soil moisture due to slower growth rates that occur only under drought stress. This corresponded to higher chlorophyll content and photosynthetic rates, less kernel abortion, and a higher harvest index than wild type following drought [149].

In conclusion, the understanding of stress-responses in plants is still rather sketchy, and yet the message from "stress-breeding" efforts is clear: interconnected multilayer control networks operate in highly plastic, fast-responding genetic control systems [16]. Ongoing projects will also tell us what precisely goes wrong with bioproductivity under stress when agricultural practices neglect/disturb basic ecosystem functions and cycles. Strategies to cope with the effects of abiotic stresses on yield performance need to combine short- and long-term approaches. The short run consists in making appropriate choices of cultivars or species and cropping settings in order to limit the timing and intensity of the stress experienced by the plants (i.e. water or nutrient deficit avoidance) ([154] and refs therein). For longer term solutions, integrative approaches associating QTL combinations, phenotyping, modelling, and transgenic approaches for identifying traits associated with yield potential and stress adaptation are needed [151,170].

7. Agro-evo-devo, from domestication to "imaginomics"

The genetic diversity within landraces and wild relatives is mined in traditional crop breeding to find yield-enhancing genes. For some crops valuable genes may now be mined out. This creates a "genetic glass ceiling" that impedes future increases in yield [9,171]. The advent of genetic engineering, in combination with systems biology, offers novel routes through the glass ceiling (see Section 4) [9], as truly dramatic yield increases may require comparably dramatic changes in crop plants.

Transformation of the teosinte ear to that of maize offers an illustrative example of the magnitude of changes that are possible, and also of the difficulty of bringing about such changes through genetic engineering. The teosinte ear consists of a linear array of seeds, each encased in a stone-hard hollow formed by the rachilla (stem) of the ear and by a hard bract [172]. The rachilla breaks apart at maturity so each hard case, with its enclosed seed, is dispersed. Teosinte is not a practical source of grain because the hard case surrounding each seed makes further processing difficult. Indeed, the current theory suggests teosinte was originally domesticated for immature ears and for the sugar contained in the stem before flowering, not for grain [172].

The maize seed must be exposed to be useful as a grain, not borne inside a hard covering as in teosinte. This transformation was mediated by change in a single gene, *tga1* [173]. Maize alleles of *tga1* have only seven fixed DNA differences from teosinte alleles, but this is enough to reduce the size of the hollow in the rachilla so the grains lie outside the hollow, making the grain accessible for food [173]. Other effects of this maize allele include reduced glume size, a thinner lignified layer in the glume, and reduced silica deposition in the glume [174]. Presumably, this mutation arose among teosinte plants that were already in cultivation, and the mutant plants were noticed and preserved by the people cultivating the plants [172]. A single gene can mediate enormous change. Indeed, much of the variation between maize and teosinte is controlled by only 5 loci [175].

Could modern people bring about comparably major changes in plants to generate new, major food crops? Discovery of mutant teosinte plants bearing the useful *tga1* allele presumably took many years of cultivating large numbers of plants, until the rare, lucky mutation occurred and was observed and preserved. Preservation may have been facilitated by its partial dominance [174], but many domestication mutations are recessive, and hence are more difficult to interpret and preserve. One may search for useful variants among wild species, but major changes of value to agriculture may be detrimental to wild plants, and so removed from wild populations by selection. These include such crucial features as loss of dispersal mechanisms (e.g., loss of shattering at seed maturity), loss of seed dormancy, reduced levels of toxins, and higher allocation of resources to reproduction instead of competition with other plants. This creates a low glass ceiling for possible domestication [9].

Genetic engineering offers the promise of radically transforming plants, but to make such changes the genetic engineer must figure out what alterations in plant genes could achieve the desired results. That is not easy. Even with the discovery of the fixed sequence changes in *tga1* it is not clear how that allele causes its observed effects in teosinte-maize. Devising such an altered allele from scratch would, at present, be impossible. The detailed mechanisms of gene function and organismal development still contain far too many black boxes to allow prediction of gene function from DNA sequences without much prior information. Instead, genetic engineers typically work with genes whose function(s) were previously discovered through standard developmental genetics and/or biochemistry. We know of no successful attempt to make predetermined changes to plant morphology using a newly created gene. On only a few occasions have genetic engineers modified enzymatic activity using selection combined with mutation and/or recombination of gene fragments [176], where a particular function such as enhanced function of an enzyme has been achieved.

At present, plant genetic engineers commonly make minimal changes in plants, typically inserting only a single gene that makes a protein of value, such as the BT toxin gene (to protect against insect herbivores) or an EPSP synthase enzyme not inhibited by glyphosate, conferring resistance to glyphosate herbicide [177]. Note that the BT toxin gene was found, ready-made, in bacteria, where its insecticidal properties had long been studied. Moderately glyphosate-resistant EPSP synthases were first generated, with great difficulty, by mutagenesis of sensitive enzymes, but were eventually replaced with enzymes found in bacteria, in particular, from an *Agrobacterium* strain isolated from a waste-fed column at a glyphosate factory [177,178]. Forced evolution within that highly artificial environment yielded a better enzyme than the more directed work of many scientists. Subsequently, gene shuffling was used to generate an effective enzyme to detoxify glyphosate [179]. The ability to kill weeds but not crops resistant to glyphosate has proved immensely useful, even obviating the need for ploughing to control weeds, thus reducing soil loss. Weeds have also been evolving resistance to glyphosate, or acquiring resistance by introgression from crops. Agronomic practice cannot remain fixed for long; agronomy must endlessly improve to keep ahead of the evolution of weeds [9].

The few attempts at morphological modifications of plants have been simple. Fields of *Brassica napus*, oil seed rape, turn bright yellow from the showy flower petals held above the leaves, but these petals can block nearly 60% of the photosynetically effective light, and also facilitate entry of fungal pathogens [180]. Specification of flower organs is the best understood aspect of plant developmental genetics [181], and *Brassica* is a close relative of *Arabidopsis*, the premier plant genetic model. With only a slight extrapolation from previous developmental genetic experiments in *Arabidopsis*, *Brassica napus* lines were generated with petals converted into sepals, which are small and block little light [180]. This increases photosynthesis and reduces disease, improving yield. Subsequently, a *Brassica napus* line was found that completely lacked petals with no other deleterious effects [182]. It was mutated in a previously unstudied gene, whose function is still not understood. Hence, this clever piece of genetic engineering has been supplanted by a spontaneous mutation. That a mutation in an unknown gene would confer such a desirable phenotype, in the best-studied developmental genetic pathway, exposes the great holes in our understanding of how genes generate phenotype. We are not close to fathoming the complexities of developmental control systems. The ability to insert genes into plants far outstrips the ability to evaluate and predict the effects of novel genes.

Consider an analogy to the computer revolution: modern people would likely say that the year 1965 was "before computers," but if one were to time-travel to a university in 1965 and make the same comment, people might respond, indignantly, that there IS a computer at this university; it occupies much of the computer centre building. Little would they understand the pervasiveness and power of computers in the 21st century. Equivalently, people in the future may look back to 2013 as "before genetic engineering", not because it is unknown at present, but because it is now relatively feeble and unimportant compared to future applications [183].

Three possible avenues for making dramatic changes to plants are (1) introducing or greatly modifying biosynthetic pathways, (2) changing the resource allocation by the plant, and (3) changing the morphology of the plant. The latter two cases have been illustrated in the rice section. Each of these would likely require introducing or modifying multiple genes. How could one figure out what to do?

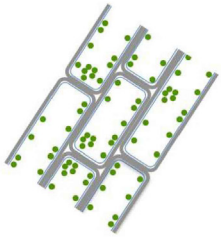
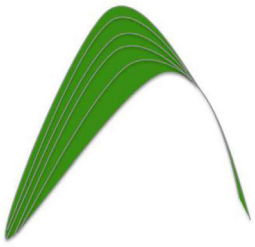
The vast diversity of plants provides very many examples showing how evolution has achieved such changes. There are very many cases of parallel evolution, in both physiology and in morphology, that illustrate alternative methods of achieving comparable change. The scientific field of the Evo-Devo seeks to understand how gene changes bring about evolutionary innovations. A mechanistic understanding of evolutionary change may show how genetic engineers could make comparable useful changes in existing crop plants or in potential crop plants [183]. For example, in Section 5.1 we discussed the more efficient C4 photosynthetic system and the ongoing attempts to convert C3 plants to the C4 system. Furthermore, biosynthetic pathways for secondary compound production may also be useful targets for genetic manipulation. Most plants produce secondary compounds that have roles in plant development and in the interaction of plants with their ecological environments, notably in defence against pests [43,184]. These complexities must be considered before biosynthesis of such compounds is engineered into novel plants [184,185]. Secondary compounds can be very effective: people extract pyrethrins and nicotine from plants and use them as insecticides. The evolutionary arms race has equipped some insect pests with the ability to sequester or to inactivate some secondary compounds. This is an example of evolutionary specialization by the insect. If production of the most effective secondary compounds could be moved into distantly related crop plants, it is unlikely that the pests of the crop plant could quickly deal with the newly introduced secondary compounds, which they would perceive as completely novel. It is also unlikely that pests of the source plant for the secondary compound would be adapted to the different morphology and life history – and pre-existing secondary compounds – of the crop plant [183]. Secondary compounds that have stood the test of evolutionary time, with few insects acquiring resistance, might prove agriculturally effective for longer than some human-developed insecticides, to which pests have already become resistant (e.g., DDT). Caffeine is another fascinating example (see *supplemental file S3*). Caffeine synthesis, moved into tobacco, does protect against tobacco pests [186]. Synthesizing such chemicals does have a cost to the plant, which must be judged against the benefit, and we must avoid possible toxic effects on people or our animals.

A straightforward approach to create new agricultural crops could be informed by the remarkable genomic synteny among related taxa. For example, the grass family has a highly conserved arrangement of genes along substantial chromosome segments [187]. This facilitates identification of orthologues of domestication genes already discovered in grass crops; the orthologues in non-crop species could be targets for modification, in hopes of achieving comparable changes, allowing domestication. The gene controlling seed shattering in sorghum, *sh1*, has three different inactivating mutations in various landraces, indicating independently acquired mutations [188]. The rice orthologue and both maize orthologues have mutations that reduce expression and contribute to lack of seed shattering. This shows that orthologues across the grasses can contribute in the same way to domestication. The wild ancestors of grain crops shared a number of features that facilitated their domestication. These plants were annuals with high resource allocation towards seed production and generally large seeds [189]. Generating new domesticates using comparable gene changes would probably only succeed on wild plants that also have similar features of annual habit with high resource allocation towards seed production. There are many plant families and genera that include species with a range of life history strategies, from perennial climax community plants to annual herbs. Such differences are concomitant with altered resource allocation, with annuals directing more resources to reproduction. Comparison of related species with different life history strategies might help elucidate genetic changes that control resource allocation, allowing genetic engineers to increase allocation to seeds in potential crop plants.

For other applications one might want to steer resources to vegetative growth, for example, in trees grown for wood production or biomass for biofuels. This might be achieved by manipulating the phase of growth of the plant. Only after the phase transition to a potentially reproductive state can a plant make flowers. The genetics of phase change is under study in model plants [83], and may inform methods to prevent the switch to the reproductive phase in trees for lumber production. This could also prevent the escape of transgenes into wild populations. (If vegetative propagation proves uneconomic, one might use an inducible form of the phase-change gene to allow seed production only by specific individuals, or the anti-phase change system might require crosses between two mutant lines, for example, in dioecious trees such as *Populus*, allowing controlled seed production on an isolated island.)

No one has yet tried to make major changes in plant morphology through genetic engineering, like the major change between teosinte and cultivated maize. Only the simple change of dwarfing in oilseed rape (*Brassica napus*) has been achieved by genetic engineering, and this did increase yield [190]. Yet dwarfing had already been achieved by standard breeding methods. Dwarfing was crucial for the green revolution; dwarf varieties of wheat and rice were crucial because they do not lodge when carrying a heavy load of grain and have greater resource allocation to seeds [9]. Some simple morphological changes can already be understood at the genetic

Table 1
Integrated levels for higher plants, from cells to the entire organism, and their relationships to plant productivity and biomass production.

Cell level	***Organ level***	***Plant level***
		
Cell number, size, and function	***Organ size and identity***	***Plant biomass***
Genome size	Growth rate & size	Architecture, height, organ type and number
Ribosomes	Cell cycle, differentiation/ Endoreduplication	Meristem specialization, determinate/ indeterminate growth
Photosynthesis	Identity: stem cells, leaf, seed, fruit, storage organs	Vegetative/reproductive transition; circadian clock
Cell proliferation and expansion	Cell elongation, secondary wall formation (cellulose and lignin), vessel differentiation	Sink, source, flow systems
Pluripotency	Gene regulatory networks [1] and gene expression maps [2]	Extensive secondary growth, seasonality in perennials
Gene regulatory networks (1)	Hormone signalling and crosstalks (auxin, cytokinins, GAs, ABA, brassinosteroids, etc)	Epigenetics & chromatin regulation
	Feedbacks from growth (geometry, mechanics)	Ploidy level
		Allelic interactions at selected loci for growth rate/biomass (collective gene performance) – allele optimization
		Water and nutrient efficiency [3]
		Light interception efficiency
		C3/C4 photosynthesis
		Signal integration: stress, hormones, secondary metabolites
		Yield genes [4]

We summarise the hierarchy of factors that affect yield and related ideas discussed in this review. Developmental patterns result from dynamic internal and external cues affecting complex control systems that, in turn, determine numbers and patterns of cell divisions and differentiation and cell and organ growth and thus the plants' physiological potential for agricultural yield. Factors are listed under the level at which their effects are most pronounced.
[1] Yield Booster – Gene Regulatory Network, http://www.yieldbooster.org/intrinsic-yield/gene-regulatory-network.
[2] Gene expression maps, bar.utoronto.ca/efp/cgi-bin/efpWeb.cgi.
[3] Poplar molecular physiology, Plant Biology, 12 (2010) and the Poplar Research Group (Germany) at http://www.pappelgruppe.uni-goettingen.de/home/index_EN.html.
[4] Yield Booster – Intrinsic Yield Genes, http://www.yieldbooster.org/intrinsic-yield/intrinsic-yield-genes.

level, such as the *erecta* gene of *Arabidopsis* [191], but more complex morphological changes are currently not understood. This will be a challenge for Evo-Devo studies, but also offers great rewards.

Some alleles improve one attribute important for yield, while diminishing another. This limits what can be achieved in breeding, but in some cases it may be possible to get around even seemingly inevitable trade-offs. For example, in tomato, increased fruit yield typically correlates with lower sugar content. However, plants heterozygous for normal and non-functional alleles of the gene SFT give substantially higher yields and also have higher sugar content [89]. TILLING [192] may facilitate discovery of moderate-strength SFT alleles that confer the same benefit when homozygous, allowing true-breeding lines. Some day it may be possible to design alleles that minimize trade-offs, perhaps by manipulating relative expression levels in different tissues or at different growth stages or under different environmental conditions.

Eventually, Evo-Devo studies may lead to a systems-level understanding of how the genome achieves the phenotype of the plant. That might allow genetic modifications to generate morphologies and physiologies that do not exist among any wild species. If this becomes possible, then the potential for new and modified crops could be far more dramatic.

If sorghum seeds were born on condensed lateral shoots, covered by husks, the serious problem of bird predation might be solved: this resembles the change actually achieved when teosinte was domesticated into maize [9]. One might engineer plants to have multiple morphotypes or "physiotypes" that could adapt to different regions or to unexpected weather variations that would doom standard crops [9]. Some wild species grow in a wide variety of habitats, so this may be possible. More fanciful goals might include changed morphology to facilitate harvest, such as strawberries that, when ripe, are lifted above the plant on vertical stems, with the berry pointing up, so a harvester with closely-spaced fork-like tines could sweep over the field and harvest them. Instead of producing cotton from cotton plants, one might engineer plants with much higher yield to make masses of very long cotton-like trichomes, for example, on a narrow maize ear covered by huge husks.

There are large regions of the land surface not currently used for agriculture, because they are too dry or too cold for standard crops. Yet all but the very driest regions support dense vegetation. Perhaps plants already adapted to such habitats could be modified to produce food. The useful product need not be seeds, but could be a novel organ, e.g., modified from leaves or shoots, borne in a position and at a time to facilitate harvest. Any specific imagined plant of this type would likely be as wide of the actual future as the fantasized robots of 1965 differ from the iPhones, iPads and personal computers of today. But the potential for innovation in biology is probably as large or larger than that of computer technology.

8. Conclusions and perspectives

Biological productivity, often taken for granted, remains elusive for a major reason: we need to understand it as an emergent property of living systems involving multiple levels of organization at the same time (Table 1 illustrates this point and summarizes this review). The notion of bioproductivity has been considered here in a much broader sense than previously. The efficiency of biological processes, the mechanisms generating morpho-functional and metabolic adaptations and diversity are have been integrated to the concept of bioproductivity. We conclude that plant productivity in general is astonishingly adaptive and robust. We have highlighted the main trends as known today, but one additional component may need consideration in the future: the extraordinary pluripotency of higher plants. The breakthrough study in *Arabidopsis* has just given the first inkling [193] of what may become possible and opens a route to cell fate transition design [194,195]. The next step is to strengthen the idea that productivity and biomass production only make sense when considered at several widely different scales: planetary (biospheric), (agro)ecosystemic and the organismal levels.

The future of the world depends on adequate agricultural production to satisfy human needs. Malthus has not yet been defeated on the human needs versus agro-ecosystem ceilings.

Note added in proof

Specialized membrane transporters offer multiple avenues for significant crop improvement (Schroeder et al [196]). These include better resistance to aluminum toxicity and salt toxicity, allowing agriculture on degraded soils, improved resistance against pathogens, and improved absorption of nitrate from soils, for more efficient fertilizer use. Nutritional value for human consumers can also be improved, for example, using transporters that pump iron or zinc into organs consumed by humans.

Acknowledgements

The presented work has been to a great extent inspired by seminars and discussions with colleagues and students participating for the Masters advanced course "Bio-resources and biodiversity" at ENS de Lyon (http://biologie.ens-lyon.fr/masterbiosciences/presentation-des-ue-1/les-ue-europe/biodiversity/). We are thankful to all of them. We are deeply thankful to the anonymous reviewers who guided us through this vast research area and helped us keeping the main facts in the right focus. The financial support from the Plant Reproduction and Development (RDP) laboratory at ENS de Lyon and from the Institut universitaire de France (IUF) have been essential to this project. I.N. is a fellow of the IUF and the Michel Serres Institute (http://michelserresinstitute.ens-lyon.fr). S.d.B.d.R has been a fellow in the region Rhône-Alpes PhD program.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.plantsci.2013.05.010.

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