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Need for multidisciplinary research towards a second green revolution

Commentary

Bernd Wollenweber¹, John R Porter² and Thomas Lübberstedt¹

Despite recent achievements in conventional plant breeding and genomics, the rate of increase of crop yields is declining and thus there is a need for a second green revolution. Advances within single disciplines, alone, cannot solve the challenges of increasing yield. As scientific disciplines have become increasingly diversified, a more complete understanding of the mechanisms by which genetic and environmental variation modify grain yield and composition is needed, so that specific quantitative and quality targets can be identified. To achieve this aim, the expertise of plant genomics, physiology and agronomy, as well as recently developed plant modelling techniques, must be combined. There has been recent progress in these individual disciplines, but multidisciplinary approaches must be implemented to tackle drought stress and salinity as major constraints to achieving sufficient grain yield in the future.

Addresses

¹The Danish Institute of Agricultural Sciences, Department of Genetics and Biotechnology, Research Centre Flakkebjerg, Slagelse, DK-4200, Denmark

²The Royal Veterinary and Agricultural University, Department of Agricultural Sciences, Højbakkegaard Alle, Taastrup, DK-2630, Denmark

Corresponding author: Wollenweber, Bernd
(bernd.wollenweber@agrsci.dk)

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Introduction

Despite the rapid development of new technologies, for example in the area of plant genomics, a crucial question that needs to be asked is whether the rate of increase in crop yield will be sufficient to feed the world population, which will increase from about 6 billion in 2000 to more than 10 billion in 2050 [1], given an ever decreasing area of arable land. Projections from the Food and Agriculture Organization (FAO) indicate that the average world cereal yield would have to reach 5 t ha⁻¹ from its present level of 3 t ha⁻¹ to do this [1]. Because drought and increased salinisation of arable land could result in a 50% land loss by the year 2050 [2], increased water-use efficiency and salt tolerance are important challenges for agricultural production [3–5].

In the mid-twentieth century, overall food production in the developing countries could keep pace with population growth because higher-yielding crop varieties were introduced in the ‘green revolution’ [6]. To date, conventional breeding has led to a continuous increase in seed yield, which has generally resulted in an increased harvest index and improved yield stability. Long-term selection experiments indicate that there is a sufficient potential for genetic improvement of quantitative traits over many generations [7]. However, there is evidence for declining crop yield increase [6,8], which will result in a gap between demand, caused by population growth, and the amount of available food.

The genetic research approach has led to the identification of quantitative and qualitative traits and has elucidated their structure–function relationships. In the agronomic and crop-physiological approach, experiments to evaluate the effects of climatic variability and agronomic factors on yield and on quality parameters have been investigated. However, scientific disciplines have become increasingly diverse and there is a declining commitment to funding research on whole-plant physiology or on crop breeding [9]. It is foreseeable that advances within a single discipline alone cannot solve the challenges of increasing crop yield potential. We summarize recent progress in individual disciplines and advocate a multidisciplinary approach based on plant genomics, physiology and modelling to tackle drought stress and salinity as major constraints to achieving sufficient grain yield.

Progress in plant genomics

The ambition of plant genomics [10] is to provide structural information about whole genomes, and in multi-parallel experimental approaches to gain a holistic view of biological processes, to accumulate information across experiments and species in order to investigate the function and the interaction of genes, and to transfer information to crops by transgenic approaches or by creating ‘designer’ plants [11] on the basis of functional DNA markers [12].

For major crops, more than 300 000 gene-derived expressed sequence tag sequences have been generated. To date, complete plant genomes have been sequenced for the model species *Arabidopsis thaliana* and for rice [13,14]. In view of improving complex traits, such as grain yield, this structural genomic information has two major implications. For those species that have complete

genome sequence information available it has become feasible to apply the 'forward genetic' approach of map-based gene isolation, as compared with previous attempts in which it was impossible to go beyond mapped quantitative trait loci (QTL). The second major implication is the possibility of information transfer between related species owing to the evolutionary conserved gene order that occurs in chromosome blocks or even in chromosomes [15]. This concept for the identification of orthologous sequences has successfully been used in several studies [16,17].

Efficient tools for multi-parallel and rapid testing of gene function include microarray-based expression profiling [18], comprehensive mutant collections and virus-induced gene silencing [19]. Complementary tools are under development at the protein and the metabolite level [20]. For *A. thaliana*, the ambition is to characterize the function of all genes of this species by 2010. The term 'function' relates to the basic characteristics of genes (e.g. mutant phenotype, biochemical properties and expression pattern of selected genotypes). Functional genomics will rapidly provide new candidate genes for several traits owing to the better understanding of their biochemical role. However, a holistic understanding of traits such as grain yield will require inclusion of the complex field situation, which strongly depends upon environmental factors, genotype by environment (GxE) interactions, and the genetic background. A major challenge remains to establish association of allelic (for several loci) and trait variation [21], in view of varying environmental factors that are present under field conditions, to allow prediction of the agronomic potential of genotypes on the basis of their DNA sequences.

Progress in physiology and agronomy

Physiological studies have contributed to our knowledge of the variability of environmental and agronomic constraints, and of how these constraints interact, for plant phenology, canopy development, biomass production and crop yield. Recent qualitative and quantitative crop physiological approaches have advanced our understanding of inter- and intra-specific variation in how yield is affected by supply of both nutrients and assimilates, affecting source strength and/or sink capacity, during different phenological phases [22,23]. Essential functions within the plant such as nutrient uptake, transport and assimilation have been characterised in roots, shoots and leaves [24,25]. Studies on structure–function relationships of the regulation of plant metabolism have linked molecules, proteins, enzymes and metabolic pathways to organelles, cells, organs and the whole plant [26,27].

We have increased insight into the responses of crops to various external and internal factors, including abiotic and biogenic stress events as well as climate change [28,29]. However, little is currently known about the interaction

of these stress episodes and the effect of multiple stress events [30,31]. Diverse stress conditions often activate mechanisms of adaptation and acclimation. Adaptation is related to heritable modifications in structure or function. Molecular control mechanisms for abiotic stress tolerance are based on the activation and regulation of stress-related genes (e.g. those encoding antioxidants, compatible solutes and heat-shock proteins) [2]. Acclimation is defined as the generation of non-inheritable modifications that reflect the structural and physiological plasticity of the plant. Here, investigations of posttranslational modifications of enzyme activity have underlined the metabolic plasticity of crops in coping with external constraints to biomass production [26,27,32,33].

Whole-plant physiology can elucidate structure–function relationships of crop traits and can analyse changes in function that are induced by different treatments and/or environments [34]. However, this has only rarely resulted in improved cultivars [9,35], partly owing to large uncertainties caused by the variability of climate and agronomical practise. Thus, further studies of the intrinsic properties of a particular organ or plant, as well as of extrinsic constraints that influence its function, are needed to manipulate and to predict crop productivity and grain composition.

Advances in agronomy have enabled the manipulation of mineral nutrition and of nutrient-use by way of fertilizer application strategies, thereby affecting key biochemical and physiological processes such as photosynthesis, carbohydrate and nitrogen metabolism [36–38]. Progress in this area has also resulted from increased knowledge of crop protection and the use of decision-making systems, as well as the development of suitable technology to implement these decisions, for example in the area of fertilizer application in precision farming using satellite navigation systems [34,36].

Progress of modelling

Crop simulation modelling is one of the original manifestations of the concept of systems biology. It was 'systematised' by adopting the cybernetic concepts and language of systems analysis [39] and applying them to fundamental plant processes. By integrating knowledge from soil science, crop physiology and meteorology into mathematical equations, crop models are able to simulate and to predict the growth, development, yield and quality of cultivars and species [40–44]. Thus, crop models have a quantitative heritage, they recognize the need for reductionist knowledge, and are one of the most important tools in biology to bridge and to make operational the dialogue between reductionism and holism [45]. In addition to the application of models to the soil–plant–atmosphere system and to plant growth and development at a whole-plant and canopy level [46–49], there have been recent approaches to model plant metabolism at a cellular level [50,51] and to quantify metabolic fluxes through major

biochemical pathways [27,52,53]. Also, attempts have been made to understand stress responses to, for example, water deficits [54,55] (see note added in proof).

Differences in the performance of crop varieties within models are described by the use of cultivar-specific parameters, detailing, for example, threshold photoperiods and temperatures that define the equations to predict the rate of crop development. Such parameter values are assumed to reflect genetic differences between cultivars, but they are determined without complete knowledge of the metabolic pathways from gene to product that leads to a given phenotypic response. Until recently, there has been only little relation between these parameters and genotypes, and gene-based approaches to modelling have not received much attention because there has been a lack of dialogue and sharing of concepts between modellers and molecular geneticists [56–59]. Yin *et al.* [35] describe a methodology by which QTL information can be incorporated into crop models. Their suggested method is to, first, create a crop model that predicts complex traits on the basis of relationships between elementary processes and environmental variables. One can then evaluate the capability of the model to predict the complex trait across a wide range of G×E combinations and identify QTL for model-input traits by use of a genetic QTL approach. By doing this a QTL-based model can be developed in which the original values of model input traits are replaced by QTL-based inputs. One can then validate the QTL-based model across environments.

The next stage would be to characterize crop varieties in terms of the QTLs for grain proteins and to then attempt to predict the total protein contents and fractional distributions for new environmental conditions on the basis of this understanding. Other recent QTL-based modelling studies have included an attempt to predict barley yields for inbred lines [60]. It is likely that future profitable lines of inquiry will need to examine individual growth and developmental processes.

Multidisciplinary approaches

Our understanding of the mechanisms that determine crop productivity, yield and resource-use efficiency is advanced, but insufficiently exploited in agriculture [36]. Closing the ‘yield gap’ and increasing yield stability under different stress conditions are of great importance for securing food and feed availability. Thus, the identification and elimination of bottlenecks of plant development under stress conditions is of pivotal interest. Drought has become the single most limiting factor to crop production worldwide [61] and the need for a ‘blue revolution’, in which the water-use efficiency of crop plants is improved, has been highlighted [62]. In (semi-)arid regions, evaporation of water from irrigated soils has resulted in the accumulation of salts and has led to the development of saline soils. Salt stress leading to water

deficits, ion imbalances, as well as to damaging effects of salt itself, and will ultimately affect crop productivity [63,64].

There have been advances in our understanding of the physiological responses of plants to water deficits, such as the interaction of chemical and hydraulic signalling that affects crop development and yield [65]. Target traits for genetic engineering and/or marker-assisted selection to improve water-use efficiency are stomatal conductance, hormones, osmotic regulation, root morphology and flowering time [5]. Recent modelling has simulated the effect of water deficit on crop production [54,55]. However, because salt tolerance is a complex trait, attempts to improve salt tolerance by way of conventional breeding have had only limited success [64,66]. The multigenic nature of salt tolerance, established by QTL and microarray studies [64,66–69] complicates the identification of both key loci within QTL and of candidate genes. Salt-tolerant plants (halophytes) are physiologically adapted to high salt concentrations, and compatible solutes such as sugars, organic acids, and amino acids that are used in osmoregulation could provide the first biochemical indicators of salt tolerance for genetic exploitation [63,64].

Understanding of the genetic potential of plants with regard to stress tolerance at the DNA level would be a key step towards more efficient and targeted breeding. The genetic potential of genotypes within species depends upon their particular allelic composition. Knowledge of the association of alleles at relevant loci with target traits would allow description of plant potential on the basis of their genetic composition. However, these associations cannot be established for all possible genotypes (there is combinatoric restriction in the case of 50 000 genes that have two or more alleles per locus). Therefore, the genetic potential assigned to particular polymorphisms within genes in single genetic experiments needs to be re-evaluated and approved over time.

Once biochemical pathways are established and connected to events at cellular, organ and plant levels, it might be possible to predict the phenotypic effects of polymorphisms. Assignment of genes to pathways on the basis of their expression patterns might help to identify the best candidates in which to search for relevant polymorphisms that affect traits of interest. Furthermore, meaningful controlled conditions can be provided to screen the responses of different genotypes to stress factors, taking into account G×G and G×E interactions.

The interplay between simulation models and molecular genetics will be required in the future because these two methods satisfy complementary issues in trying to dissect and predict G×E interactions. Yin *et al.* [35] state the issue precisely when they conclude, “Geneticists and physiologists have interests in common, such as G×E.

Traditionally, physiologists cannot afford to carry out detailed experiments on complex traits with many genotypes, whereas geneticists working with many genotypes cannot afford to go into much physiological detail". The rapid development of new research instruments is providing scientists with opportunities to work more closely together. This should result in more insights into GxE interactions, narrowed genotype–phenotype gaps and effective ‘breeding by design’.

Conclusions

Genomics, proteomics and metabolomics will increase our understanding of the regulation of different physiological processes, the development of organs and the resistance mechanisms that are activated in response to stress. However, they must be integrated into the plant — from the organ level to the plant and canopy level — before they are beneficial. Future breeding paradigms could be characterized by multidisciplinary ‘joint’ efforts. The joint activity could be used to create a common platform for addressing complex questions, in which modelling could play a crucial role in integrating the knowledge chain in plant biology at either the lower point (systems biology) or the higher point (crop physiology). For this to happen, scientists from crop physiology, molecular genetics and genomics should rethink the research agenda to create opportunities to make genomics work to increase crop production. Two conditions exist before this knowledge fusion can occur. The first is that molecular geneticists and crop modellers learn each others ‘language’. The second is that funding agencies actively support joint interdisciplinary research activities, rather than merely paying them lip service as has clearly been the case in the past. Molecular genetics risks running into an intellectual dead-end if the issue of scaling to the crop level is not grasped; cooperation with physiologists and modellers can provide the means to overcome this.

Note added in proof

Since submitting the review, we have become aware of a paper that illustrates an approach to modelling plant traits that includes traits that are relevant to performance in dry conditions [70].

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