Meeting the Global Food Demand of the Future by Engineering Crop Photosynthesis and Yield Potential

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Increase in demand for our primary foodstuffs is outstripping increase in yields, an expanding gap that indicates large potential food shortages by mid-century. This comes at a time when yield improvements are slowing or stagnating as the approaches of the Green Revolution reach their biological limits. Photosynthesis, which has been improved little in crops and falls far short of its biological limit, emerges as the key remaining route to increase the genetic yield potential of our major crops. Thus, there is a timely need to accelerate our understanding of the photosynthetic process in crops to allow informed and guided improvements via in-silico-assisted genetic engineering. Potential and emerging approaches to improving crop photosynthetic efficiency are discussed, and the new tools needed to realize these changes are presented.

An Emerging Yield Gap

Nothing is more important to human health and well-being than an adequate supply of food in terms of nutrition and calories. Although a significant proportion of the global population has suffered malnutrition over the last 50 years, it has been the result of failures in access to food, not in its global production. Indeed, over this period, we have seen surpluses of the major crops, which make shortages a very distant concern for most of the population. The most important primary foodstuffs, in terms of millions of metric tons (Mt) produced in 2013, were maize (1,018 Mt), paddy rice (746 Mt), wheat (713 Mt), and soybean (276 Mt) (Food and Agriculture Organization of the United Nations, 2015). These four crops account for about two thirds of calories consumed globally (Ray et al., 2013). Moreover, the average global yield per unit area of land (t/ha) for each of these crops has more than doubled since 1960, as illustrated for rice and wheat (Figure 1). So why bother worrying about food security now? One reason is that these global surpluses in staple crops have influenced the progressive decline in spending on plant science research and crop improvement, evident at the global level (Beintema and Elliott, 2009). However, this shift in funding may be myopic in the face of current global population and food consumption trends. Notably, the global population is expected to increase from just over 7 billion today to 9.5 billion by 2050, a 35% increase (USCB, 2015). An increasing proportion of the population will be urban, resulting in diets shifting increasingly from staples to processed foods, fortified with more meat and dairy products, which require large amounts of primary foodstuffs to produce. For example, 10 kg of feed is required to produce 1 kg live cattle (Smil, 2000). Thus, an increase in urban population will result in an increased demand for high-quality animal products, requiring an increase in crop production that is substantially faster than that estimated based solely on the projected population growth. This trend is expected to continue, and it is predicted that the world will need 85% more primary foodstuffs by 2050, relative to 2013 (Ray et al., 2013).

So is our current rate of increase in crop yields sufficient to meet this rising demand? It doesn't seem to be the case. If current rates of crop yield improvement per hectare are simply maintained into the future, supply will fall seriously below demand by 2050 (Figure 1; Ray et al., 2013). The resulting rise in global food prices may have the largest impact in the poorest tropical countries, which have the highest population increases. A compounding factor is that improvement in subsistence crops in these tropical countries is even slower than in our four leading crops. For example, the global average increase in yield per hectare of cassava, a major staple for sub-Saharan Africa, between 1960 and 2010 was 63%. This is less than half of the 171% increase for wheat over the same period (Figure 1). The problem is further compounded by the fact that the rate of improvement in yield of even our major crops in some areas of the globe is stagnating or even moving into reverse (Long, 2014; Long and Ort, 2010; Ray et al., 2012). Indeed, China, India, and Indonesia are the world's largest producers of rice, where yields per hectare across these countries increased by an average of 36% between 1970 and 1980 but only by 7% between 2000 and 2010 (Long, 2014). When faced with such numbers, one may rightfully ask: why are yield improvements stagnating?

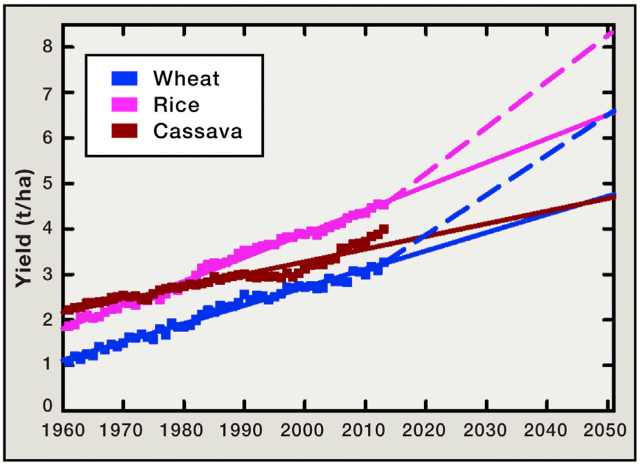

Figure 1. Annual Average Global Yields of Cassava, Rice, and Wheat from 1961 to 2013
Annual average yields for the entire globe in metric dry tons per hectare for each year from 1961 to 2013 for cassava, rice, and wheat (Food and Agriculture Organization of the United Nations, 2015). Solid lines are the least-square linear regressions fitted to these data and projected forward to 2050. The broken lines indicate the projected demand for rice and wheat, after Ray et al. (2013). The original data for cassava were provided as wet weight and are corrected here to dry weight, assuming a 70% water content.

Stagnation in Yield Improvement and Photosynthesis

The gains of the Green Revolution were achieved largely through improved genetics coupled with the enhanced agronomy and crop protection that allowed realization of the higher genetic yield potential. We can begin to understand these gains by defining them in mathematical terms. Yield potential (Y_p) is the mass of harvested material per hectare of land that a genotype of a crop can achieve in a given environment in the absence of biotic and abiotic stresses. Improved Y_p was achieved during the Green Revolution, in particular by selecting genotypes that partitioned more of their biomass into the harvested product. For example, the selection of dwarfed genotypes of wheat resulted in more biomass in the grain and less in the stem. This proportion of a plant's biomass that is invested into the harvested product, e.g., the grain of rice, is termed the partitioning efficiency or harvest index (ε_p). To a first approximation, the yield potential of a given genotype is then the product of the solar radiation received over the growing season by a unit area of land (Q) and the efficiencies with which the crop intercepts that radiation (ε_i), converts the intercepted radiation into biomass energy (ε_c), and then partitions the biomass into the harvested part of the plant (ε_p):

$$Yp = Q.\varepsilon_i.\varepsilon_c.\varepsilon_p........ \quad \text{(Equation 1)}$$

With reference to this equation, the Green Revolution increased ε_i and ε_p. In fact over the past 50 years, harvest index (ε_p) has almost doubled in the major grain crops and now stands at ~0.6 for modern cultivars of rice, wheat, and soy (Long et al., 2006b; Zhu et al., 2010). However, if these plants are to retain the structural components of the stems and ear or pod casings to support the seed at harvest, there is little prospect of further genetic improvement for this component of the equation. Similarly, interception efficiency (ε_i), that is the proportion of the visible sunlight that is intercepted by the crop over the growing season, has reached 0.8–0.9 for modern crop genotypes. Again, this suggests that this determinant of yield potential is also very close to its biological limits (Zhu et al., 2010). The one area in which there has been little or no improvement is in conversion efficiency (ε_c) of visible solar energy, which remains at about 0.02, and roughly one-fifth of the theoretical efficiency of 0.1 for C3 crops such as wheat and rice or 0.13 for C4 crops such as maize and sorghum (Zhu et al., 2008, 2010). Indeed, as it is clear that 50 years of conventional plant breeding has greatly improved ε_i and ε_p but not ε_c, this component of the equation appears to be a promising focus for further enhancement of yield potential.

Conversion efficiency depends on the efficiency of the process of photosynthesis, net of respiratory losses by the crop. Concern over global climate change motivated many studies of the effects of elevated CO_2 on crop production and photosynthesis. CO_2 is a limiting substrate for photosynthesis in C3 crops, so the primary effect is to artificially boost photosynthetic rate. Invariably, this results in increased yield (Ainsworth and Long, 2005; Kimball, 1983; Long et al., 2004, 2006a), demonstrating that there would be a clear benefit to yield if total crop photosynthesis could be increased genetically in crops (Long et al., 2006b). Yet, this also begets the question: if photosynthesis has such a strong influence on crop yield, why have traditional breeding and selection for higher yield delivered no or very small improvements in photosynthetic efficiency? There are several reasons for this effect. Within a crop species and its relatives, there is huge variation in ε_i and in factors affecting ε_p, such as the proportion of biomass invested in leaves during vegetative growth, rates of leaf growth, size of leaves, and leaf longevity. This has provided breeders with much variation in selecting for improved ε_i and ε_p. By contrast, the process of photosynthesis is highly conserved, not only within a crop species, but across a wide range of plants. Further, directed efforts have screened for germplasm with high light-saturated photosynthetic rates at the leaf level, and selection here has often been at the expense of other traits. For example, selection for higher light-saturated rates of leaf photosynthesis alone has often indirectly selected for lower total leaf area, offsetting any advantage at the crop level (Long et al., 2006b). This approach also ignores the fact that about half of crop carbon gain occurs under light-limited conditions (Long, 1993). How can we then approach increasing photosynthetic efficiency, and why might this be a timely strategy for a second Green Revolution when it was not for the first one?

Three factors make improving overall crop photosynthetic efficiency a possibility today. The first one is based on our understanding of the photosynthetic process. In the 50 years since the start of the first Green Revolution, knowledge of the photosynthetic process has exploded. From light capture by pigment molecules to production of storage carbohydrates; this fundamental process for all life on Earth is now understood in great detail. For higher plants, some algal species, and photosynthetic prokaryotes, not only is every step known, but the structures of the key proteins have been unraveled to high resolution to reveal the mechanism of their action, while the genes coding for the key components have been characterized. This includes