

Rice and global food security: the race between scientific discovery and catastrophe

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In this chapter we describe the factors contributing to the almost insurmountable problem of feeding the explosively growing populations of Asia in an unpredictable world of climate change, and we offer a solution. Crop production is simply the product of land area multiplied by yield and given the absence of new land for agriculture, we focus on yield.

Background

Elite rice cultivars, which dominate the food supplies of the millions of poor people in Asia, have approached a yield barrier that is set by the efficiency of solar energy conversion in photosynthesis (Kropff et al. 1994; Sheehy 2001; Sheehy et al. 2007a). The yield gains made from the Green Revolution technologies, centred on canopy architecture, crop nutrition and crop protection, have been fully exploited and rice production is slowing (Dawe 2007). Agriculture must be about providing sufficient food for all human beings, thus balancing supply and demand, in a manner that is sustainable economically, socially and environmentally. To guarantee that this demand can be met, scientists must explore ways to break yield barriers by maximizing the efficiency with which crops convert absorbed solar energy into grain. Ignoring the opportunities provided by the most recent scientific discoveries would condemn billions of people to lives of hunger and misery. We hope to demonstrate the urgency of using cutting-edge science and the tools of molecular biology to boost yields of rice by 50% during the next decade and thus prevent a looming catastrophe. Nonetheless, it should be remembered that we are working with plants whose patterns of growth have been shaped by millions of years of evolution and natural selection so that our scope for making improvements is probably limited to those mechanisms already tested somewhere in biology by evolution.

Generalities

Life on Earth ultimately depends on the peculiar combination of energy from the sun, the molecular composition of the atmosphere and the physical and chemical structure

of Earth's surface materials. The surface of Earth is 71% water and 29% land. A little over a third of the land is suitable for agriculture; the rest is ice, desert, forest or mountains unsuitable for farming. Crops act as intermediaries between natural resources and human life. They extract the molecules they require for synthesis from both the soil and the atmosphere and use solar energy to fuel that synthesis. Photosynthesis is the pivotal mechanism underpinning life; it transforms solar energy absorbed by plants into chemical energy by using carbon dioxide and water to manufacture carbohydrates. The productivity of agriculture is determined by land under cultivation, crop yield, solar radiation, water, temperature, crop management and agricultural research. Rice, wheat, maize, millet and sorghum provide 70% of the calories and up to 90% of all protein consumed by the world's population. About 60% of the world's population has rice as the staple cereal and almost all of the 600 million tons of rice produced each year are consumed direct by humans. During the past three years the price of rice has doubled (http://www.fao.org/es/esc/en/15/70/highlight_533.html).

The challenge of global food security

Currently, productive agriculture is successful in maintaining food security because (1) modern crop varieties grow rapidly and turn a large proportion of the plant into the harvested component; (2) fertilizer can be supplied, and irrigation in some regions; and (3) crop protection from weeds, pests and diseases is highly developed. These are all features of the Green Revolution, which greatly increased cereal production from the 1970s to the 1990s.

Today, 75% of the world's 6.7 billion people live in the developing world, where most of the world's existing poverty is concentrated. A billion people live on less than a dollar a day and spend half their income on food. Some 854 million people are hungry and each day about 25 000 people die from hunger-related causes. In the past 200 years the global population has increased explosively, going from 791 million in 1750 to a predicted 8.909 billion by 2050. At the same time the urban population has grown from 3% to about 50% of the total. About a billion people live in very large cities; 428 cities have populations greater than a million and 25 cities have more than 10 million (Brinkhoff, 2005). Each year, a city of a million people consumes about 0.75 million tons of food and 117 million tons of water (Stanners and Bordeau, 1995). In addition, about 1.5 billion tons of water (rainfall or irrigation) are also used in producing the food for that city. Currently, about 3.2 billion people are urban and require 2.4 billion tons of food each year. By 2050, the urban population will have grown and about 3.6 billion tons of food will be required.

In 1843, when the first agricultural research station was founded at Rothamsted in the UK, the world's population was about 1.2 billion people and about 4.0 ha of farmland were available per person for food production. By 2050, each person will have about 0.5 ha of farmland available. Land under rice cultivation forms about 3% of the world's farmland, with each hectare in Asia providing food for 27 people. By 2050, that land will have to support closer to 40 people. The Green Revolution more than doubled the food supply in Asia in 25 years, with an increase of only 4% in net cropped area (Lipton 2007; Rosegrant and Hazell 2000). But the area available for rice cultivation is likely to decrease. Land is taken out of cultivation for industry and housing as urbanization proceeds, poor irrigation practices or sea-level rise produce

soil too salty for rice, water scarcity prevents irrigation in places, and opportunities are few to take new land into agriculture given the need to conserve forests and biodiversity. Increased production must come from higher yields per unit area, more tonnes per hectare. The conclusion that yield increases are crucial for future food production is inescapable.

Agriculture is the indispensable base of modern society and the continuity of civilization depends intimately on the relationship among agriculture, water and climate. Over the next 40 years, climate change could result in more frequent extremes in weather and cause adverse shifts in the world's existing climatic patterns. The first half of the 20th century showed a warming trend virtually worldwide. The second half was characterized by a tendency toward short-lived extremes of record-breaking proportions. For example, the lowest temperature ever recorded in England was -26.1°C on 10 January 1982; 21 years later, the highest temperature was recorded (38.5°C on 10 August 2003). If climate change causes extreme variation in weather, so that climate becomes a less useful concept for farmers, agriculture could cease to be an industry with predictable outputs. Such a future would put enormous pressure on modern society.

To achieve global food security in the future, production of food must increase by at least 50% from 2008 to 2050, when the global population is expected to reach a plateau of 9 billion (Royal Society 2009). A 50% increase in 42 years requires a compound rate of increase of 1% per annum, which appears easy until we remember that it must be a consistent increase every year, and that it must be achieved on less land, using less water, with less fertilizer and pesticides, probably with less labour, and ideally with much less oil for machinery, all under a changing climate. Godfray et al. (2010) provide a comprehensive and authoritative review of this problem and discuss five strategies that should be adopted: closing yield gaps (i.e., helping farmers reach yields much closer to those on research stations), increasing productivity, reducing waste, changing diets and expanding aquaculture. The changes must also be sustainable economically, environmentally and socially in the long term (Royal Society 2009). The heavy dependence of productive agriculture on fossil fuel, and on finite sources of rock phosphate for fertilizer (Gilbert 2009), must be tackled.

Rice, wheat and maize are the predominant cereals that feed the world, each with 600–800 million tonnes produced annually. Barley is a distant fourth (around 140 million tonnes) and the minor cereals such as sorghum and millet, while locally important, amount to less than 7% of global production (FAOSTAT 2009). Thus, rice, wheat and maize comprise the premier league, and rice contributes the most as human food because some wheat and much maize are fed to livestock and some maize goes for industrial use (starch, oil) and, increasingly, for biofuel (ethanol).

About half the world's population depends on rice, especially in Asia, which accounts for 90% of production. Rice is grown and eaten on every inhabited continent and is becoming more popular rapidly in Africa. Perhaps because rice is mostly eaten cooked as whole grains, more attention is paid to the type and quality of the grain compared with other cereals. Even consumers in developed Western countries, who eat comparatively little rice, know of long grain, pudding, risotto, basmati and fragrant rice. In Asia rice is deeply embedded in the culture and consumers take great interest in the storing, cooking and eating properties of the rice

they buy. There is active research to improve the nutritional quality of rice, including its content of zinc or iron (www.harvestplus.org), and vitamin A (Tang et al. 2009). Given the nutritional and cultural importance of rice, there is no prospect that this cereal will diminish in global importance.

We believe that a vital contribution to food security will come with improvement in the productivity of rice crops, underpinned by the necessary scientific research.

Water

Of the water on Earth 97% is seawater and 2% of the remaining water is locked up in ice at the poles. Competition is rising for the remaining 1% of fresh water, which is needed not only for agriculture and human consumption but also for industry. There is a biophysical relationship between the biomass of crops and their water consumption. Given the food demands of the current 6.7 billion inhabitants of the planet, it is not surprising that agriculture accounts for about 70% of all fresh water used. Significant decreases in that fraction will threaten the productivity of intensive agriculture.

Rice is grown on around 160 million hectares, under four main agro-ecosystems (Rice Almanac 2002). Irrigated rice, in level fields maintained shallowly flooded for most of the growing season, occupies about half the area and provides 75% of production. Rain-fed rice (in flooded fields as far as rainfall permits) is the second most productive system, on one-third of the area, giving nearly 20% of production. Flood-prone rice and upland rice produce less than 10% of global production. Upland rice (grown like an ordinary crop without standing water) is notably low yielding (1–2 t/ha) and largely a crop of subsistence farmers on marginal land with infertile soils, erratic rainfall and troublesome weeds. Without improvements in the yield capacity of the irrigated rice system, the challenges of meeting future demands for rice cannot be met.

Current concerns

Of more immediate concern than the issues surrounding food security in 2050 is the plight of the 1 billion people in the world (nearly 15% of the population) who live in poverty now. About 70% of them live in Asia, with rice as their staple cereal. Improved productivity of rice crops is vital here because it contributes in several direct and indirect ways to alleviating poverty (Dawe 2000, 2007). Higher yields give poor farmers a better income, and also keep the market price of rice low, thus making it more affordable to the urban poor. Improved productivity is a requirement for every rice agro-ecosystem: in irrigated and rain-fed rice, it can make a large increase overall in the world's rice crop, and, in flood-prone and upland rice, higher yields help at the household scale to lift subsistence farmers out of poverty.

Failure to reduce poverty in the near future and to secure a food supply for 9 billion people by 2050 will be a catastrophe for the next generation. Productive and sustainable rice crops have a large part to play in this, underpinned by scientific discoveries to be made and applied as quickly as possible. Catastrophe in the 1960s was averted by the Green Revolution, in which research and development by the International Rice Research Institute (IRRI) was prominent. After 50 years of activity, IRRI is continuing to apply 'rice science for a better world'. Having established a firm context in the social sciences for increased rice productivity as the key objective, we turn now to the biological science necessary to make progress.

Crops and resource capture

It had been known for centuries that climate, weather, soils, nutrients, crop duration, water and management were the principal determinants of yield. The discoveries of science and technology in the last 250 years have provided good understanding of how plants grow in relation to their environment (Begon et al. 2006). We can think of a crop as a mechanism for gathering dispersed or dilute resources: solar radiation, carbon dioxide, water and mineral nutrients. Resources are consumed so that what is taken by one plant is not available to another. Solar radiation and water are dispersed in space and time, carbon dioxide is a trace constituent of the atmosphere and mineral nutrients are in dilute solution in the soil. The biochemistry of the crop plant processes the resources to make crop biomass, part of which is harvested as cereal grains, potato tubers, apples, flax stems for fibres and so on. Other environmental factors are conditions, experienced but not consumed, such as temperature, pH and salinity of the soil. Temperature is especially influential, constraining crop occurrence to sites suitable for arable agriculture and to growing seasons, and controlling crop growth through rates of growth and development. Nevertheless, the gathering of resources is paramount. Productive agriculture maximizes the resources gathered by the crop by eliminating competition from weeds and by minimizing losses of processed resources to pests and diseases.

Rice cultivation provides many examples of how farmers and researchers have ensured that the crop gathers resources effectively and converts a large proportion into grains for harvest (Greenland 1997). Rice varieties since the 1960s have been bred for short straw and upright leaves to intercept maximum solar radiation. Of equal value is the ability of short-stemmed crops to take up more nitrogen without growing too tall and becoming susceptible to lodging (falling over), and the storage of nitrogen in the shaded lower leaves, which is later transferred to the filling grain (Sinclair & Sheehy 1999). Modern rice varieties produce grain as half the above-ground biomass, which is probably the maximum feasible given the need for a canopy of adequate size to intercept solar radiation and stems stout enough to support a high yield of grain.

Techniques of cultivation that evolved over thousands of years and have been developed systematically in the last 100 years lead to effective gathering of resources. Terracing of fields and irrigation where possible provide sufficient water (and the rice plant is adapted to this in having air spaces throughout the plant that allow oxygen to reach the roots). Mineral nutrients can be supplied as residues from the previous crop, from animal manure and from industrial fertilizers. Nitrogen can also be provided by biological nitrogen fixation in the soil or irrigation water; so far as the first is concerned, bacteria or cyanobacteria convert nitrogen gas into forms usable by plants, with these microbes being either free-living or in symbiosis with green plants such as legumes or the water fern *Azolla pinnata*.

Solar energy: the power source for crops

Solar radiation is a dispersed resource that cannot be gathered by any practicable means for supply to a field crop. Instead, farmers maximize production by using land area, the sunniest seasons, and crop durations of sufficient length to accumulate intercepted solar radiation. For example, in tropical climates where temperature permits crop growth throughout the year, multiple rice cropping is practised and the

highest yield comes from the crop grown in the dry season, which receives the most solar radiation. This is made possible by irrigation since rainfall alone would normally be insufficient for growth of an annual crop in the dry season.

Solar energy absorbed by plants powers their growth, whereas solar energy that passes unintercepted by leaves to the ground is energy lost to the crop. A well-managed crop is a community of plants that rapidly grows sufficiently dense so that the leaves of the community absorb all of the incident solar radiation. Consequently, for most of their existence, crop plants are members of a dense community in which they compete with their family members and neighbours for resources. The properties of that community limit the expression of an individual's potential growth and yield, but the collection of limited individuals maximizes the yield of the community per unit ground area. Crop management is about balancing the attributes of the individual with the properties and requirements of the community to produce a yield acceptable to farmers.

Solar energy captured in photosynthesis gives individual plants the capacity to synthesize, organize and maintain the range of structural units required to produce grain. However, photosynthesis follows a law of diminishing returns with the amount of incident solar radiation. Erect-leaved crops solve that problem by spreading radiation down into the darker interior of the crop canopy (Sheehy and Cooper, 1973). There is a limit to the population density of individual plants. Each productive individual plant must capture sufficient solar energy to enable it to produce an acceptable quantity of grain. Sharing the incident solar energy among the individuals limits each one of them, but allows the community to intercept the available solar energy with greatest efficiency. Once the solar energy is absorbed by an individual plant, it is converted into chemical energy in photosynthesis. It follows that the more efficiently the photosynthetic system of a plant converts solar energy into chemical energy, the greater is the potential growth rate of the individual.

The flow and use of energy captured by an individual are directed by control mechanisms, some of which must ultimately be peculiar to the genome of an individual species. Those mechanisms dictate plant morphology, anatomy, physiology and the pattern of growth in a given climate. The mechanisms are the product of evolution and natural selection and must have guaranteed survival in a world of competition for resources. Nonetheless, the traits guaranteeing 'survival of the fittest individual' may not be the most suitable for high productivity in intensively managed crop communities of fairly homogeneous, weak individuals.

Carbon dioxide: a very dilute resource

In contrast to water and mineral nutrients, carbon dioxide cannot be collected and concentrated for supply to a crop at the field scale. Carbon dioxide is a resource universally available at the prevailing atmospheric concentration, 380 ppm, give or take some diurnal and seasonal fluctuations. We rely on the mechanisms of photosynthesis and stomatal opening, that has long been honed during evolution, to maintain a diffusion gradient down which carbon dioxide moves rapidly into the leaf for fixation by photosynthesis into carbohydrate. (Stomata are the pores with controllable apertures on the surface of leaves that allow exchange of gases with the atmosphere.) This is facilitated by adequate water supply for transpiration so that the stomata remain fully open, and by sufficient mineral nutrients, especially nitrogen

for the biochemical machinery of photosynthesis. The principal photosynthetic enzyme, Rubisco (ribulose 1,5-bisphosphate carboxylase–oxygenase), is needed in large amounts and accounts for up to 30% of the nitrogen in rice leaves. This in large part explains why productive crops require a substantial supply of nitrogen.

Photosynthesis

In the majority of plants, including rice, the CO₂ that diffuses into the leaf is first fixed into a compound with three carbons (C₃) by the photosynthetic enzyme Rubisco – this is known as C₃ photosynthesis. Rubisco is inherently inefficient because it can also catalyze a reaction of its substrate with oxygen in the air, giving a wasteful process known as *photorespiration* (rather than *photosynthesis*). At temperatures in excess of 20 °C, there is increasing competition by O₂, with a dramatic reduction in CO₂ fixation and photosynthetic efficiency. Thus, in the hot tropics where most rice is grown, photosynthesis becomes extremely inefficient.

The C₄ pathway involves the initial fixation of atmospheric CO₂ into C₄ acids using an enzyme that is insensitive to O₂. In the next stage of the pathway, CO₂ is released from the C₄ acids for fixation by Rubisco. The two stages are spatially separated, allowing a high concentration of CO₂ in the vicinity of Rubisco. The build-up of CO₂ by this ‘CO₂ pump’ requires extra energy from sunlight and therefore it is only in warm climates that the C₄ pathway is beneficial. The two stages of C₄ photosynthesis are partitioned in morphologically-distinct photosynthetic cells. In C₄ grasses such as maize and some C₄ dicots, enlarged bundle sheath (BS) cells surround the vascular bundles or veins (V) and the BS cells are then surrounded by mesophyll (M) cells. Each pair of veins is thus separated by two bundle sheath and two mesophyll cells in a V–BS–M–M–BS–V pattern referred to as Kranz anatomy. Furthermore, the specialized organelles (chloroplasts) carrying out photosynthesis are very different in these two cell types. Mesophyll cell chloroplasts support the capture of CO₂ by the C₄ cycle, whereas BS chloroplasts support fixation of CO₂ by Rubisco. The anatomy of C₃ plants is typically a V–BS–M–M– ... –M–M–BS–V pattern, with variable numbers of mesophyll cells, usually in the range 4–12. The BS cells are smaller than in C₄ plants and they contain few chloroplasts.

Radiation-use efficiency and yield

Monteith (1977) found that the dry weight of the crop above ground (biomass) was proportional to the intercepted solar radiation accumulated during the crop’s life. The constant of proportionality is a measure of how effectively biomass was produced from each unit of solar energy intercepted; it became known as radiation-use efficiency (RUE, although usually quoted in units of gram dry weight per MJ radiation). The value of RUE for a crop was more or less constant during vegetative growth provided that the crop was adequately supplied with water and mineral nutrients. Monteith (1978) compared the yields of a number of C₃ and C₄ crops growing over a range of crop durations and suggested that C₄ crops could produce about 66% more biomass than C₃ ones in the hot developing countries of the world. Given that rice is mostly grown in the tropics and subtropics, where C₄ crops such as maize, sorghum and sugar cane thrive, it does seem surprising that rice is C₃. Although there is much variation in values of RUE measured in different

experiments, a consensus has emerged (Kiniry et al. 1989, Mitchell et al. 1998) that C_4 crops have much higher RUE values than C_3 crops, eg maize 50% higher than rice.

During vegetative growth, biomass accumulates from the carbon dioxide captured during photosynthesis and transformed to carbohydrate and other substances, minus the losses of carbon dioxide from respiration necessary to maintain the plant and provide energy for growth. Differences in photosynthesis between various crops largely explain the characteristic values of RUE for crops. The maximum yields and radiation-use efficiencies of rice and maize growing unrestricted by water and nutrients in the dry season in the tropics were measured concurrently (Sheehy et al. 2007b). The radiation-use efficiencies of maize and rice were 4.4 g DW MJ^{-1} and 2.9 g DW MJ^{-1} , respectively; the ratio of the values being 1.52. (Here the measurement of intercepted radiation was of the wavelengths usable in photosynthesis, known as photosynthetically active radiation – PAR.) At 14% moisture content the grain yield for maize was 13.9 t ha^{-1} and for rice was 8.3 t ha^{-1} ; maize, the C_4 crop, outyielded the C_3 crop by about 67%. This result is consistent with the results published by Monteith (1978). If we convert the photosynthetic system of rice from the C_3 form to the C_4 form, maximum yields should increase by about 5 t ha^{-1} (50%). A huge added benefit of the C_4 system in rice would be the doubled water-use efficiency that accompanies the trait. The benefits for the poor of such an improvement in the face of increasing world population and decreasing natural resources would be immense.

Scientific discoveries needed for C_4 rice

Research over the last 40 years has established why some C_4 plants, including maize, are especially productive. The biochemistry is not novel: the same enzymes and pathways occur in C_3 plants in small amounts for housekeeping. During evolution of C_4 plants, there has been duplication of the genes and then specialization of the enzymes to operate in different conditions with much greater throughput. The critical achievement is raising the concentration of carbon dioxide around Rubisco by spatial separation of initial and final fixation of carbon dioxide into two adjacent cells, with rapid diffusion of metabolites through many plasmodesmata (tiny channels of cytoplasm through the cell walls). This is achieved through specialization of the bundle sheath cells and proliferation of vascular bundles so that every mesophyll cell is next to a bundle sheath. The mesophyll cells have also become specialized, for instance, in lacking Rubisco in their chloroplasts.

As a C_3 plant, rice has none of these anatomical changes. Important discoveries must be made in what controls the spacing of vascular bundles, and how bundle sheath and mesophyll cells become highly specialized in their biochemistry and also linked by abundant plasmodesmata. Once these discoveries are made, the C_4 syndrome can be introduced into rice so as to supercharge its photosynthetic system and thereby boost its radiation-use efficiency and yield (Mitchell & Sheehy 2006, Sheehy et al. 2007a).

Conclusions

In well-managed crops, in which the fraction of grain per unit of biomass has been maximized, future yield improvements must be accompanied by increases in radiation-use efficiency. In the review of Mitchell et al. (1998), the data suggested that maize (C_4) had radiation-use efficiency 50% greater than rice, a C_3 crop in a tropical environment.

The simple model in that review led to the suggestion that rice photosynthesis would have to be converted from the C_3 to the C_4 syndrome to achieve yield increases of 50%. Sheehy et al. (2007b) went some way to confirming this conclusion when they reported that the difference in the yields of rice and maize crops grown without limitations of water or nutrients at IRRI was 5.6 t/ha. Furthermore, although C_4 plants display plasticity (Sage and McKown 2006), their C_4 nature is not lost during plastic responses to the environment. The attraction of the full C_4 system is not only its high productivity and yield but also the better use made of water and nitrogen. No known non- C_4 solution offers this complete package of benefits.

Supercharging photosynthesis is the only way to improve yield potential substantially in rice while not increasing the demand for water and nitrogen. This means adding the C_4 biochemical pathway and modifying leaf anatomy so that the C_4 system works at its best. We are confident that now is a pivotal time for harnessing all current progress in understanding C_4 photosynthesis and in techniques of genetic engineering to try to construct a C_4 rice. To do this, partnerships are required between institutions with the specialized expertise, and that is why IRRI formed the C_4 Rice Consortium (<http://beta.irri.org/projects15/en/c4rice>) and attracted funding from the Bill & Melinda Gates Foundation.

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