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CHARTING NEW PATHWAYS TO



RICE

EDITED BY J.E. SHEEHY,
P.L. MITCHELL, AND B. HARDY

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The responsibility for this publication rests with the International Rice Research Institute.

Mailing address: DAPO Box 7777, Metro Manila, Philippines

Phone: +63 (2) 580-5600

Fax: +63 (2) 580-5699

Email: irri@cgiar.org

Web: www.irri.org.

Rice Knowledge Bank: www.knowledgebank.irri.org

Courier address: Suite 1009, Security Bank Center

6776 Ayala Avenue, Makati City, Philippines

Tel. +63 (2) 891-1236, 891-1174, 891-1258, 891-1303

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CHARTING NEW PATHWAYS TO C₄ RICE

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EDITED BY J.E. SHEEHY, P.L. MITCHELL,
AND B. HARDY



2007

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IRRI

INTERNATIONAL RICE RESEARCH INSTITUTE

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Foreword

Agriculture is the indispensable base of human society and the nature and productivity of agriculture are determined by water and climate and largely directed by the products of agricultural research. Today, the world's population is 6.6 billion, and 5.1 billion live in the developing world where most of the world's existing poverty is concentrated. Currently, a billion people live on less than one dollar a day and spend half their income on food, 854 million people are hungry, and each day about 25,000 people die from hunger-related causes. The United Nations Millennium Declaration, agreed upon in September 2000, commits the world's nations to "eradicate extreme poverty and hunger." Solving the current problem would be sufficiently challenging, but what makes it even more daunting is that several aggravating features are magnifying. Over the next 50 years, the world population will increase by about 50% and climate change will probably result in more extreme variations in weather and cause adverse shifts in the world's existing climatic patterns. Water scarcity will grow and the demand for biofuels will result in competition between grain for fuel and grain for food, resulting in price increases. Furthermore, 75% of the world's people will live in cities, whose populations will need to be largely supported by a continuous chain of intensive food production and delivery. All of these adverse factors are occurring at a time when the developed nations are both reducing their investments in agricultural research and turning their remaining research investments away from productivity gains. If all of this weren't bad enough, the elite rice cultivars that dominate the food supplies of the millions of poor people in Asia have approached a yield barrier and production growth is slowing.

Each hectare of land used for rice production in Asia currently provides food for 27 people, but by 2050 that land will have to support at least 43 people. Feeding the 5.6 billion Asians in the 21st century will require a second Green Revolution to boost yields by 50% using less water and fertilizer. Theoretical models have been used to examine this problem and they suggest that this can be done only by increasing the efficiency with which photosynthesis uses solar energy. Fortunately, evolution has provided an example of a much more efficient photosynthetic system (C_4) than that possessed by rice or wheat (C_3). Maize, for example, is one of these C_4 plants. Boosting the photosynthetic efficiency of rice by changing it from C_3 to C_4 photosynthesis

will be like supercharging a car's engine by fitting a new fuel injection system. Until the era of modern plant breeding, including genetic engineering, this was thought to be an intractable problem; now, there are many reasons for being optimistic about finding a solution. The chapters in this book are written by world-renowned experts and each of them offers special insights into the various forms of C_4 photosynthesis and how they might be introduced into rice.

The imperative for this project is necessity rather than curiosity. It will take an international consortium of research institutions to make C_4 rice a reality over the next 10 to 15 years. To that end, IRRI has formed a C_4 Rice Consortium to stimulate and conduct the research needed to invent C_4 rice. I am delighted to be able to use IRRI's resources to provide initial funds and we hope that donors will provide the support necessary to complete this important task.

ROBERT S. ZEIGLER
Director General
International Rice Research Institute

Preface

Rice displays a biphasic growth pattern: half the first phase of vegetative growth precedes the second phase of reproductive growth. The rates at which the phases proceed are strongly influenced by temperature, which largely accounts for different crop durations in temperate and tropical environments. The second phase begins when the rate of vegetative growth reaches a maximum and it reaches a maximum when the rate of growth of the vegetative phase falls to zero. During the first phase, full light interception is reached and the reservoir of nutrients for use in the second phase reaches a maximum. During the second phase of growth, the reservoirs in the vegetative portions of the crop are depleted and the second phase comes to a halt when the crop is mature: the time when most grains are filled and the fewest have been shed. Both empirical and theoretical investigations suggest that the maximum fraction of a crop's total biomass that can be grain is about 50%.

Solar energy captured in photosynthesis over the duration of a crop gives it the capacity to grow. The upper limit to crop biomass is determined by the laws of thermodynamics and mass conservation. At the limit, the total biomass is simply a function of the total quantity of solar energy captured and the efficiency with which that energy is made available for synthetic processes. Total solar energy absorption is largely a function of canopy architecture and crop duration. The efficiency of energy use is largely determined by photorespiration, dark respiration, and losses of biomass that occur owing to senescence. Canopy architecture is usually thought of in terms of leaf erectness and, given that plant breeders have selected for erectness over the past 30 years, little more can be gained in that direction. The opportunities for reducing dark respiration are very limited and senescence is essential in terms of recycling essential nutrients from the vegetative portions of the crop to the reproductive ones. There are many evolutionary examples of plants that have eliminated photorespiration by concentrating CO_2 around the photosynthetic enzyme Rubisco using a four-carbon acid (C_4) cycle. Plants such as rice that do not have a concentrating CO_2 mechanism fix CO_2 into three carbon acids (C_3 plants); their photosynthetic rates in hot environments are about half that of C_4 plants. C_4 plants have double the water-use efficiency of C_3 plants, and use about 40% less nitrogen to achieve 50% higher yields. Evolution

has made it clear that photorespiration can be eliminated; therefore, it is the obvious candidate for work aimed at significant increases in yields.

The repeated evolution of C_4 photosynthesis indicates that it should be feasible to create C_4 rice plants by engineering C_4 genes into C_3 rice and replicating strong selection pressure for C_4 traits that we think exist in nature. The development of the C_4 system can be seen as an addition to the C_3 system and it is now clear that the C_3 and C_4 syndromes are not as rigidly separated as was first thought. The enzymes that are prominent in the C_4 pathway also exist in C_3 leaves although with very low activity. More surprisingly, there is a well-developed C_4 pathway in certain locations in C_3 plants: in the green tissue around vascular bundles, and probably in rice spikelets. In the opposite direction, maize, a thoroughly C_4 plant, has patches of C_3 tissue wherever a mesophyll cell is not adjacent to a bundle sheath cell, particularly in leaf sheaths and husk leaves. Some of the wild relatives of rice have C_4 -like anatomical features and others may have CO_2 compensation points usually associated with C_3 - C_4 intermediates. When maize C_4 genes are inserted in rice, they work; the rice genome has been sequenced and sequencing of the maize genome is nearing completion. A large number of genetic resources are available for use in screening programs aimed at detecting genes associated with C_4 -ness: 6,000 wild relatives and 500,000 rice mutants. It has been suggested that *Arabidopsis* (C_3) can be used as a test system for transferral of genes from its closest C_4 relative, *Cleome gynandra*. The advantages of this are that all the knowledge of *Arabidopsis* can be used and *Cleome* has a short life cycle.

There are, of course, differences of opinion (contrasting hypotheses) between scientists as to which form of C_4 photosynthesis (single-cell and dual-cell systems) can be achieved most rapidly in rice and the ultimate effectiveness of the different forms in delivering significant increases in yield. This book explores those differences, but begins with a broad perspective of the economic problems surrounding rice and the potential impact on the poor of failing to contain upward pressure on food prices. It continues setting the scene by describing how the rice crop works and the consequences of supercharging photosynthesis.

In the second section of the book, Jane Langdale and her coauthors describe progress in various genetic approaches to understanding chloroplast development and then speculate on solutions to solving the problem of how to convert C_3 systems to C_4 ones.

The chapter of Richard Leegood examines metabolite transport and some of the structural and physiological changes that might be required when adding C_4 systems to C_3 ones.

Susanne von Caemmerer and her coauthors use models of diffusion to explore the effects of leaf anatomy and leakiness of cells on the efficiencies of the two-cell and single-cell forms of C_4 photosynthesis. Finally, they turn their attention to the anatomical and physiological requirements for C_4 rice.

Julian Hibberd advocates dual-track and fast-track approaches to the challenge of producing C_4 rice by inserting genes from *Cleome gynandra* into *Arabidopsis thaliana*.

John Evans and coauthors address the question of how the correct amounts of NADPH (biochemical reducing power) and ATP are provided in C_4 plants by two sorts of chloroplast in two types of cell. They also point out briefly the advantages of the single-cell C_4 system and identify its particular weakness (carbon dioxide leakage from the chloroplast).

The chapter by Rowan and Tammy Sage is a tour de force. It begins by identifying the essential features of a C_4 system and then examines its diversity in *Flaveria* before turning to an examination of the evolutionary factors critical to the emergence of C_4 systems. The chapter ends with a skeleton proposal on how to combine biotechnology and screening to produce C_4 plants from C_3 rice.

The genus *Flaveria* contains not only C_3 and C_4 species, but also several intermediate C_3 - C_4 species. Udo Gowik and Peter Westhoff discuss the use of *Flaveria* as a model system for studying the evolution of genes involved in C_4 photosynthesis and the subtle differences between C_3 and C_4 orthologous genes.

D.M. Jiao speculates on ways a C_4 rice could be constructed by various genetic engineering approaches.

The third section of the book is devoted to an examination of single-cell C_4 systems, how they work, and what they might deliver if engineered into rice.

Jim Burnell opens this section by reviewing the early history of attempts to increase the rate of photosynthesis by manipulating the expression of foreign genes and moves on to suggest critical issues that might be examined.

Gerry Edwards and his coauthors briefly review critical features of C_4 plants, paying particular attention to chloroplast position and differentiation in Kranz types and single-cell aquatic types. They provide a more detailed description of single-cell terrestrial C_4 mechanisms and finally suggest some single-cell models for C_4 rice.

John Raven and coauthors describe lessons relevant to C_4 to be learned from diatoms. They provide evidence of high-capacity, low-leakage carbon-concentrating mechanisms in single cells and conclude that single-cell C_4 is a viable aim in engineering C_4 rice.

Continuing with the single-cell C_4 theme, George Bowes and his colleagues describe their work with *Hydrilla verticillata*, an aquatic monocot that operates a facultative, single-cell C_4 system. Their studies suggest that, to design a single-cell C_4 rice, transporter and permeability issues as well as the nuances of enzyme regulation need to be better understood.

Christoph Peterhänsel and his coauthors suggest a novel approach to improving photosynthesis by engineering a bypass of photorespiration in the chloroplast.

The fourth section of the book covers the background of C_4 rice and how it can be delivered.

C_4 physiology is a syndrome of interrelated developmental, anatomical, cellular, and biochemical traits that almost unavoidably must rely on regulatory networks. Tim Nelson and coauthors suggest that laser microdissection of cell types and microarray profiling can provide the comprehensive data for a systems biology approach to understanding differences between rice and C_4 leaf development.

Erik Murchie and Peter Horton draw on experiences of measuring rice photosynthesis in the field and suggest that acclimation to irradiance can result from a signal provided by mature leaves, but the nature of the signal is unknown. They also explore issues surrounding the use of nitrogen for photosynthesis in Rubisco and the conflicting demands for nitrogen in the form of protein in the grain.

D.S. Brar and J.M. Ramos discuss wild species of *Oryza* as an important reservoir of useful genes. Some of these genes have been introduced into indica and japonica rice for resistance to major diseases and insects and for tolerance of various abiotic stresses. It has been suggested that the wild types may contain aspects of C_4 -ness and should be screened for anatomical, biochemical, and physiological features associated with the C_4 syndrome.

Parminder Virk and Shaobing Peng explore the consequences of inventing C_4 rice from a plant breeder's perspective. An early step would be to assess the effect of the C_4 syndrome on various agronomic traits such as resistance to pests, emergence of new pests, physical properties of the rice grains, and cooking and eating quality. Second, it would be important to evaluate the amount of expression of the syndrome in different genetic backgrounds and to identify the most promising transgenic event.

Philippe Hervé takes a genetic engineering approach and suggests that improved photosynthesis in rice can probably be achieved by engineering alleles involved in biochemical pathways and plant development. Another suggested strategy may consist of growing transgenic rice plants with C_4 features in different environments and screening for newly acquired C_4 features.

The fifth section leads the way into the formation of a C_4 Rice Consortium.

Richard Bruskiewich and Samart Wanchana deal with the role of bioinformatics in the construction of C_4 rice. They make general observations about sequenced genomes and describe a framework for gene discovery, before brainstorming on possible ways of using genomics information and bioinformatics to introduce C_4 photosynthesis into rice.

This project promises to be a universally important voyage of discovery about the most important of all plant mechanisms: photosynthesis. It will take a consortium of international institutions to make this a reality over the next 10 to 15 years. It is most encouraging that all the authors in this book have agreed to become founding members of a C_4 Rice Consortium. The next task is to build a long-term funding flow that is essential to sustaining research over the one and a half decades we estimate it will take to develop a fully functioning C_4 rice.

The book closes with a critical discussion and evaluation of the new pathways to C_4 rice. In it, all the authors highlighted important points and possibilities for success.

Section 1:

Setting the scene

How the rice crop works and why it needs a new engine

J.E. Sheehy, A.B. Ferrer, P.L. Mitchell, A. Elmido-Mabilangan, P. Pablico, and M.J.A. Dionora

Rice is the most important crop in the world for human food. Over the past 40 years, its production has kept pace with the increase in population. However, it is clear that the gains of the first Green Revolution are largely exhausted. Rice with C_4 photosynthesis could make a major contribution to a second Green Revolution. To assess how that change could affect rice, it is necessary to understand how the rice crop works.

In this paper, we examine the properties of individual rice plants both as single individuals and as members of dense crop communities. To estimate the potential of C_4 rice, we compare the yields and radiation-use efficiencies of maize, rice, and a C_4 weed. In that context, the properties of rice canopies with respect to the interception of solar radiation and its effect on leaf temperature are examined. The influence of sink size with respect to source strength is also discussed. It is possible that wild rice types have some of the anatomical features peculiar to C_4 plants and that the wild types may contain C_3 - C_4 intermediates. Consequently, we report results obtained from an examination of C_4 characteristics in the 22 species of wild rice.

Keywords: Rice, C_4 photosynthesis, radiation-use efficiency, leaf temperature, wild rice types (*Oryza* species)

Of the three major cereals that feed most of the world's population, rice is arguably the most important. Almost all of the 600 million tons produced each year are consumed directly by humans, unlike wheat and maize, of which much is used for animal feed or for industry. About half the world's population has rice as the staple cereal. For humans, rice production is about providing food in a manner that is sustainable economically, socially, and environmentally. For scientists, rice production should be about converting the maximum fraction of solar energy into the maximum amount of chemical energy in grain in the shortest possible time; that conversion should be achieved using the smallest amount of land, water, and fertilizer.

Table 1. Required percentage increases in rice yield likely to be required by 2050, relative to 2004, as a consequence of projected increases in population and projected climate change. The effect of population is an increase in yield in proportion to population increase. The carbon dioxide and temperature component takes into account an increase in concentration of carbon dioxide of up to 150 ppm, a change in temperature of up to 2 °C, and the effects on rice yields. The increase in yields to allow for disasters is calculated from the data for rice production over the past 40 years from the FAOSTAT database (2005).

Country	Percentage yield increase required			Total
	Population	CO ₂ + temp.	Disaster	
Philippines	62.0	4.2	30.3	96.5
China	7.7	2.4	9.4	19.5
India	51.2	5.1	35.3	91.6
Bangladesh	77.7	4.3	18.4	100.4

Source: Sheehy et al (2006).

Ninety percent of rice is grown and consumed in Asia, where more than the combined populations of the United States and Europe live on less than US\$2 a day (Cline 2004). Those Asians spend as much as 50% of their wages on rice (Dawe 2000). Over the next 50 years, it is predicted that the population of Asia will rise from 3.9 billion to 5.3 billion (UNFPA 2005). Climates are changing and many aspects of climate change such as higher temperatures and weather extremes are likely to have negative impacts on crops. Future increases in rice production will have to occur with less water, less fertilizer, and less land (Hossain and Pingali 1998, Tilman et al 2001, Evans 1998). Given the shortage of land for rice production, it is rice yields that will have to increase as a consequence of increased population and climate change (Table 1). The Green Revolution was built on breeding semidwarf cultivars that could be managed intensively with large inputs of fertilizer. The ability of that model to provide further yield increases is doubtful given that yields in many Asian countries have reached a plateau (Cassman 1999, Dawe, this volume). Indeed, yields in breeders' trials at IRRI have not increased for 30 years (Sheehy 2001a) and it has been suggested that a yield barrier has been reached (Kropff et al 1994).

In the absence of universally accepted scientific theories describing yield and its limits, disagreements about what precisely determines both biomass and grain yield are commonplace. Climate, weather, crop duration, cultivar, and management are the principal determinants of yield. Initially, the seedlings of a crop spend a brief period as individuals not limited by competition for resources from their neighbors. As a more dense community is established, the individual seedling becomes a family of tillers each bearing its own leaves and roots. For most of their existence, tillers are members of a dense community in which they compete with their family members and

neighbors for resources. The properties of that community limit the expression of an individual's potential growth and yield. For meaningful crop growth, each productive individual tiller must capture and use sufficient solar energy to produce an acceptable quantity of grain. Nonetheless, the plant density must be high enough to prevent undue loss of solar energy to the soil. 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. The attributes of the individuals themselves contribute to the rapidity with which the competitive community is developed, as well as to the productivity of the community. 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. It is solar energy captured in photosynthesis that gives individual plants the capacity to synthesize, organize, and maintain a range of structural units housing a myriad of metabolic processes (Sheehy 2001b). The flow and use of energy captured by an individual is 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 crop microclimate. The mechanisms are the product of evolution and natural selection and must have guaranteed survival in a world of competition for resources.

Much is made of the potential of the ongoing identification of plant regulatory genes following the sequencing of the rice genome. Currently, the desire to manipulate plant morphology, anatomy, and function in the interests of crop improvement and environmental protection is intense. Higher, more nutritious yields, shorter growing seasons, and greater synchrony in development and maturity are desirable. Traits guaranteeing "survival of the fittest" may not be most suitable for high productivity in intensively managed crop communities of fairly homogeneous, weak individuals. However, ignoring the possibility of transferring traits associated with high productivity across sexually incompatible crop species, such as maize and rice, would seem perverse (Brown et al 2005). In hot climates, eliminating photorespiration while simultaneously reducing nitrogen use and increasing water-use efficiency means converting from C_3 to C_4 photosynthesis (Sheehy 2001b). It would be astonishing if yield improvements in modern cultivars, of fixed duration, were unaccompanied by improvements in canopy photosynthesis (Robson 1982, Long 1999a,b). Consequently, in this paper, we present a brief analysis of how the rice crop works and we attempt to answer the question, What would be the impact of installing C_4 photosynthesis on the future of rice production?

Growth phases of rice

Rice is a weak perennial with two strong phases of logistic growth: vegetative growth followed by reproductive growth (Sheehy et al 2004a). Grain yield was shown to be strongly dependent on weather during the second phase, whereas the maximum weight of the vegetative portion of growth was shown to be largely independent of weather. Using ^{15}N as a tracer, Sheehy et al (2004b) showed that, halfway through grain filling, nitrogen was diverted to the developing "ratoon" tillers, stimulating a possible "third"

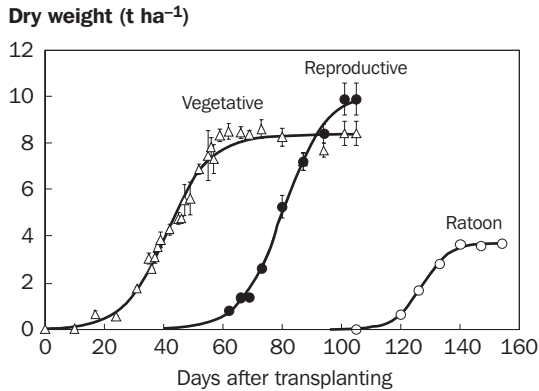


Fig. 1. The triphasic crop growth pattern for irrigated rice in the dry season at IRRI, Los Baños, Philippines. Each phase is represented by a sigmoid curve of the form $y = a/(1 + \exp[-(x - b)/c])$, where y is dry weight, x is time (days after transplanting, DAT), a is the asymptote (t ha^{-1}), b (DAT) is the time at which y is half the asymptote, and c controls the steepness of the middle portion of the curve. Coefficient values (a , b , c) are vegetative, 8.37, 41.28, and 7.45, $r^2 = 0.98$, for $x \geq 0$; reproductive, 10.20, 80.48, and 7.30, $r^2 = 0.99$, for $x \geq 40$; reproductive ratoon generation, 3.71, 127.07, and 4.56, $r^2 = 0.99$, for $x \geq 95$.

phase of growth. A triphasic crop growth pattern for irrigated rice in the dry season is shown in Figure 1; the third phase was achieved without additional fertilizer.

The influence of temperature, on the efficiency of solar energy capture and use, is difficult to describe simply because not all yield-shaping processes respond equally to temperature. Temperature can have different effects on the acquisition of resources, the loss of resources, and the efficiency with which acquired resources are transformed into products. It can also severely damage key mechanisms such as floret fertility. As a crude but useful generalization, there are three phases to the response of yield to mean daily air temperature: (1) 16–22 °C—yields rise from zero to an optimum determined by nutrients and solar irradiance (Horie et al 1995), (2) 22–32 °C—yields decline by about $0.6 \text{ t ha}^{-1} \text{ °C}^{-1}$ (Sheehy et al 2006), and (3) 32–42 °C—floret fertility falls to zero and there is a logistic decline in yield (Satake and Yoshida 1978, Sheehy et al 2006). At temperatures greater than 32 °C, additional carbon dioxide in the atmosphere accelerates spikelet sterility (Matsui et al 1997). In the temperature range of 22–32 °C, additional carbon dioxide in the atmosphere increases crop yields by about 0.5 t ha^{-1} per 75 ppm CO_2 (Baker and Allen 1993).

The grain yield equation

That mutual shading of plants in dense crop canopies leads to low yields has long been an attractive misconception (Sheehy et al 2004c). Ultimately, solar radiation is

the energy source for fueling growth and it has to be intercepted by the leaves of the canopy. There is a linear relationship between accumulated intercepted photosynthetically active solar radiation (PAR, 400–700 nm wavelength) and accumulated shoot dry weight (Monteith 1977). The slope of that linear relationship is known as the radiation-use efficiency (ϵ , g DW MJ⁻¹, where DW is dry weight). Radiation-use efficiency is not strictly a constant and is a conservative quantity, in part, because of the relative crudeness of its estimation (Mitchell et al 1998). Nonetheless, ϵ is a useful rule-of-thumb for comparing yields achieved from crops with different durations and gives some insight into whether or not there are any differences in the intrinsic physiological efficiencies of such crops. Using that concept, a simple model of grain yield can be written:

$$Y_g = H \epsilon \int_{t_i}^{t_f} I_{\text{int}}(t) dt \quad (1)$$

where Y_g is grain yield, H is harvest index (unless otherwise stated, calculated as the fraction of aboveground dry weight that is grain weight), t_i is the day of transplanting and t_f is the day of harvest, and I_{int} is the total amount of PAR intercepted by the crop. Using the data of Sheehy et al (1998), it can be shown that the harvest index of well-managed rice crops is nearly constant ($H = -0.004 Y_{\text{sb}} + 0.59$, $P < 0.01$) over a wide range of shoot biomass (Y_{sb}). The yields of crops are simply proportional to their radiation-use efficiencies when they have similar crop durations, harvest indices, and root weight ratios (Mitchell et al 1998). Given that the ϵ value of maize is about 50% greater than that of rice, Sheehy et al (2001b) suggested that maize should outyield rice by 50%.

Plasticity: properties of individuals and community members

The definition of harvest index contains no description of the individual units of production, which are the tillers. The relationship between tillering and yield in rice has been studied for over a hundred years (Inagaki 1898). Jacobson (1916) reported that increased tillering was accompanied by decreasing numbers of grains per panicle. Fifty-six years later, Yoshida and Parao (1972) observed the same inverse relationship for modern cultivars. Tillers arise from buds that develop in the axils of leaves (Robson et al 1988). For rice, the increase in numbers of tillers (with at least one visible leaf) per leaf number interval (phyllochron) on the main stem can be described by a Fibonacci series up to a given leaf number. Shading, light quality, stem elongation, and the development of the panicle as a competing sink for assimilates all lead to a reduction and an eventual cessation in the predicted rate of tiller production. For a tiller to survive, the carbon inflow must equal the carbon lost in maintenance respiration. To fully develop, the individual tiller has to be able to meet the additional carbon requirements associated with the synthesis of its various organs such as leaves and panicles (Ziska et al 1997, Baker et al 1992).

The number of tillers produced by a single seedling is strongly influenced by the density of transplanting. However, for a given cultivar, a common tiller density is often achieved independently of sowing or transplanting density (Harper 1977, Zhong et al 1999). In a field experiment, using high-yielding cultivar IR72 grown at a density of one plant m^{-2} , there were 149 tillers at maturity, giving a yield of 3 t ha^{-1} (Fig. 2A). In the same experiment, when IR72 was transplanted at 25 plants m^{-2} , there were 35 tillers per plant (875 m^{-2}) but only 27 of them were productive, giving a yield of 11.6 t ha^{-1} (Sheehy et al 2000). In contrast, new plant type (NPT) transplanted at 50 plants m^{-2} produced about 8 tillers per plant (400 m^{-2}) and the same yield of 11.6 t ha^{-1} (Fig. 2B). Clearly, the size of a tiller family depends on transplanting density and, at very low density, the number of tillers per unit ground area can influence yield. Nonetheless, in crops not limited by nutrients and transplanted at the densities used in practice, differences in tiller number per unit ground area influence yield only through differences in light interception. The later a tiller appears in the sequence of tillers that comprise a rice hill, the smaller its contribution to crop yield (Fig. 2C).

What is the link between yield, leaf area, and tiller density? At full light interception, the average leaf area of an individual tiller or plant, l_i , is given by

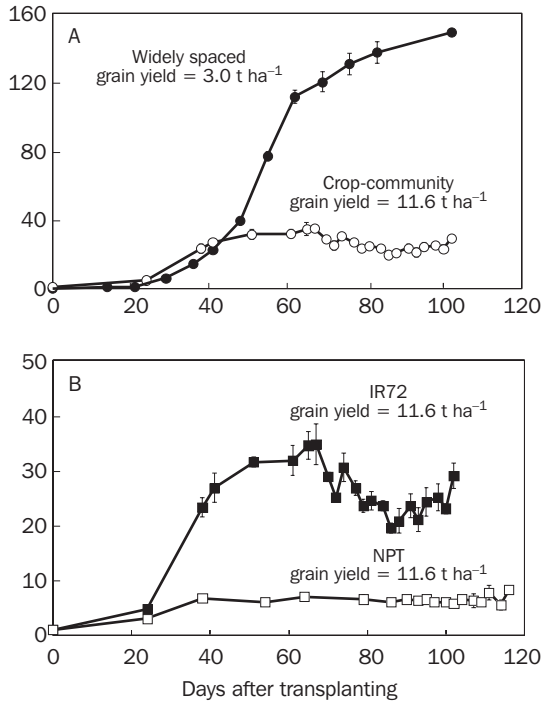
$$l_i = L_{\max}/N \quad (2)$$

where N is the number of identical tillers per unit ground area and L_{\max} is the maximum leaf area index for full light interception and yield (Sinclair and Sheehy 1999).

Using equation 2, we can calculate l_i for IR72 and the NPT when $L_{\max} = 11.2$. Assuming there are approximately 675 productive tillers per square meter (T m^{-2}) in IR72, l_i would be 166 cm^2 . For the NPT with 350 T m^{-2} , l_i would be 320 cm^2 . By contrast, for maize with the same LAI and at 10 plants m^{-2} , l_i would be $11,200 \text{ cm}^2$. Furthermore, if there are approximately 4 live leaves per tiller in rice and 10 in maize, an individual leaf of maize must be about 14–27 times larger than a rice leaf. In addition, for the same grain yield, the size of the cob in maize has to be about 35–68 times larger than a rice panicle. The detailed anatomical and biomechanical implications of changing plant size are not immediately obvious, although Niklas (1992) discussed many of the principles. In maize, Kranz anatomy and vein density may have valuable biomechanical properties in addition to those associated with the concentrating mechanism for CO_2 .

The challenge of integrating known mechanical principles into growth models was addressed by Silk (1984), who described the advantages of hollow panicles for flexural rigidity. Flexural rigidity (F) depends on Young's modulus of elasticity and that is a function of the composition of the plant tissue. Flexural rigidity is also a function of the moment of inertia and that depends on the geometrical arrangement of the material. Broader issues of mechanical strength have been addressed by Niklas (1994). However, as yet, such principles have not been consciously used to design desirable plant types. Maurice et al (1997) addressed problems relating to the biomechanics of an individual grass leaf, describing form and mass distribution. If yields are to be

Tiller number (no. hill⁻¹)



Panicle weight

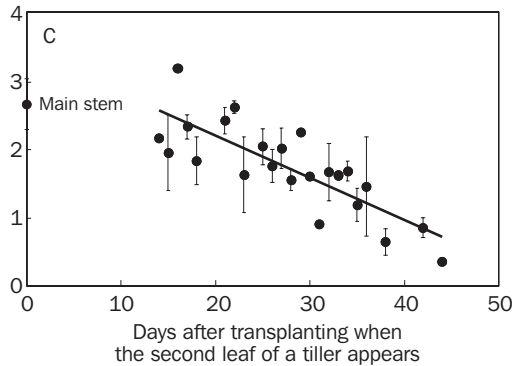


Fig. 2. (A) Tiller number of widely spaced and crop-community plants of irrigated rice IR72 in 1997 dry season; (B) tiller number of crop-community plants of irrigated rice IR72 and NPT in 1997 dry season; IR72 has the same data as in (A) plotted at higher resolution. Grain yields at 14% moisture content are shown for reference in both figures; error bars are standard error where $n = 4$. Tiller number is given as number per hill, where the hill is a planting position, normally with a single plant in experimental crops; (C) the relationship between the weight of a panicle at maturity (y) and the time after transplanting that the second leaf of its supporting tiller appeared (x); $y = -0.062 + 3.43x$, $r^2 = 0.65$. In addition, the weight of the panicle of the main stem is shown.

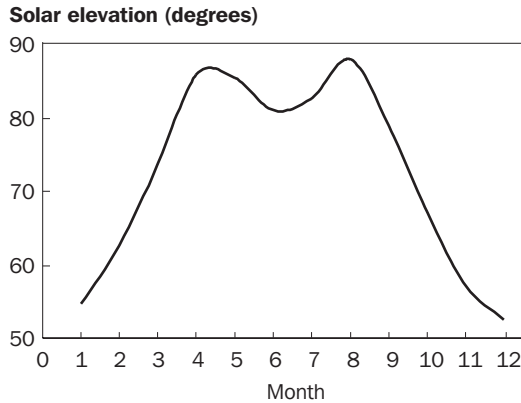


Fig. 3. The annual pattern of maximum solar elevation (mid-month) at IRRI, Los Baños, Philippines (14°11'N). Source: NOAA Solar Position Calculator at www.srrb.noaa.gov/highlights/sunrise/azel.html.

increased by 50% in a single growing season, the mechanical strength of stems and roots must be increased.

Solar radiation and canopy architecture as drivers of canopy photosynthesis

The annual pattern of solar elevation at mid-day, measured in the middle of each month, is bimodal in the tropics (Fig. 3). The monsoon climate at such a location ensures that solar irradiance can be highly variable from day to day and across seasons and years. Solar irradiances (400–2,400 nm wavelength), for the same date, in different years can vary from about 2 to 30 MJ m⁻² day⁻¹ (Fig. 4A). Temperatures at such locations are less variable, but mean values for a given day can vary by about 6 °C (Fig. 4B). The structure of a rice canopy is not uniform in the sense that each hill resembles an inverted cone with the tillers widely spaced at the top and tightly bunched near the bottom. The irradiance experienced by individual leaves depends on solar elevation, leaf depth in the canopy, erectness, and orientation to the sun. Consequently, the leaves of individual tillers experience continuous fluctuations in the energy and matter fluxes peculiar to their location in the canopy and solar elevation. Furthermore, the leaves of a rice canopy are rarely still and canopy architecture is not as uniform as theoretical models often suggest. Nonetheless, simple models of PAR distribution in canopies and its consequences for canopy photosynthesis are valuable. Two models are of interest. The first is the Bouguer–Lambert law (Monsi and Saeki 1953):

$$I/I_0 = \exp(-k_{\text{par}}L) \quad (3)$$

where I_0 is the irradiance (PAR) above the canopy, I is the irradiance (PAR) at some level in the canopy beneath a leaf area per unit ground area of L , and k_{par} is the extinc-

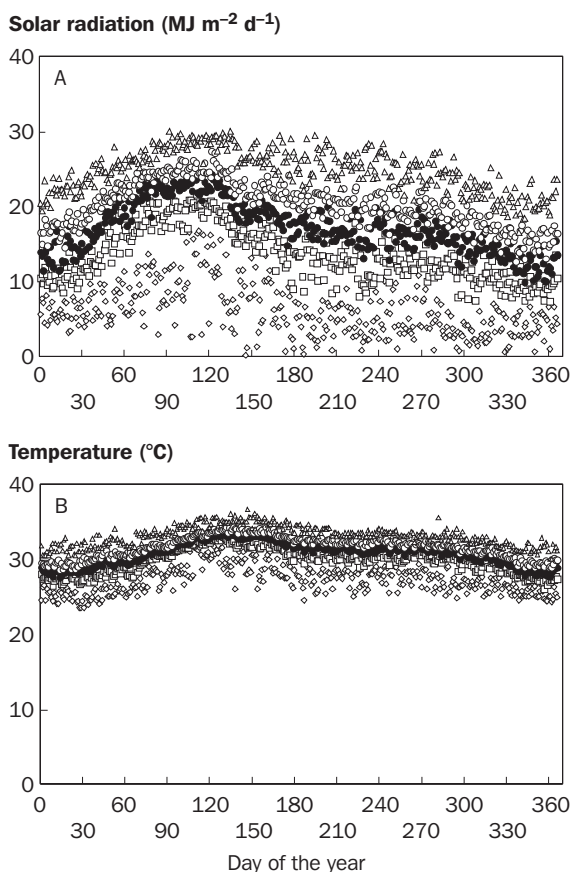


Fig. 4. Annual patterns of (A) solar radiation and (B) maximum temperature at IRRI, Los Baños, Philippines; data extracted from the IRRI weather database (1979-2005); daily median, \bullet ; third quartile, \circ ; first quartile, \square ; absolute maximum, \triangle ; absolute minimum, \diamond .

tion coefficient for PAR. Measurements of the extinction coefficient in a rice canopy show that k_{par} varies with solar elevation as shown in Figure 5; the variation is more marked in clear conditions (Fig. 5A) than in overcast conditions (Fig. 5B).

Another useful model for calculating light (PAR) distribution and canopy photosynthesis was described by Monteith (1965) in terms of the fraction of light transmitted through unit leaf area index without interception (s). The leaf area of the canopy is divided into sunlit, once-shaded, and twice-shaded leaves, that is, those receiving direct sunlight, those receiving light transmitted through one leaf, and those receiving light after transmission through two leaves. The extinction coefficient, k , and s are related by the equation

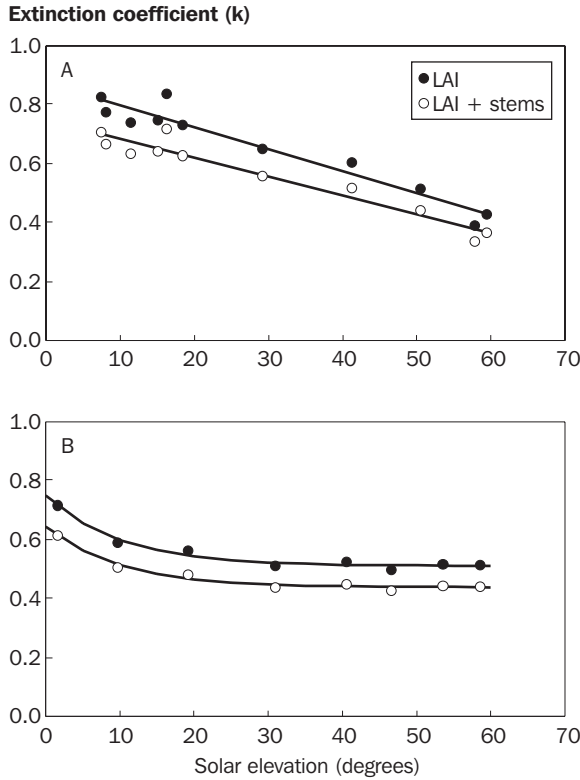


Fig. 5. Values for the extinction coefficient at different solar elevations calculated for LAI and LAI + stem area index (shoot) under (A) direct (LAI: $y = -0.0075x + 0.87$, $r^2 = 0.93$; LAI + stems: $y = -0.0064x + 0.75$, $r^2 = 0.93$) and (B) diffuse light conditions (LAI: $y = 0.51 + 0.24 \exp(-x/9.94)$, $r^2 = 0.98$; LAI + stems: $y = 0.44 + 0.21 \exp(-x/9.94)$, $r^2 = 0.98$).

$$s = [\exp(-k_{\text{par}}) - m] / [1 - m] \quad (4)$$

where m is the fraction of light transmitted through a leaf (Sheehy and Johnson 1988).

The s values for IR72 were calculated (equation 4) using the extinction coefficients for different solar elevations (Fig. 5) and a value for m of 0.1. The irradiance (PAR) above the canopy was measured on a horizontal surface at different solar elevations for clear and overcast conditions. The irradiances (PAR) of sunlit, once-shaded, and twice-shaded leaves, in the canopy, were calculated as a function of solar elevation and are shown in Figure 6. These irradiances are the values of PAR that would be measured on a surface at the same orientation as the leaf surface. In

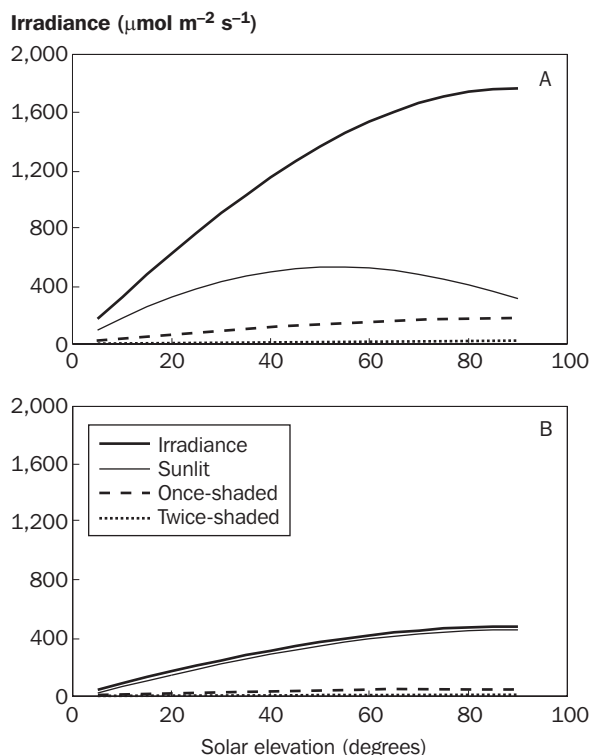


Fig. 6. The irradiances of sunlit, once-shaded, and twice-shaded leaves of an IR72 rice canopy under (A) direct and (B) diffuse light conditions for irradiance conditions in mid-April at Los Baños, Philippines ($14^{\circ}11'N$, $121^{\circ}15'E$, altitude 21 m). Note that incident PAR is for a horizontal surface, but the PAR for leaves is that calculated for a surface at the same orientation as the leaf.

clear conditions (Fig. 6A), irradiance (PAR) above the canopy reached a maximum of $1,766 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a solar elevation of 90° . The maximum irradiance (PAR) of sunlit leaves was $530 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a solar elevation of about 55° and it decreased to $312 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 90° . For overcast conditions (Fig. 6B), the irradiance (PAR) above the canopy and of nonshaded (sunlit) leaves was almost exactly the same at all solar elevations; the maximum value shown at 90° was $482 \mu\text{mol m}^{-2} \text{s}^{-1}$. The irradiances of the nonshaded (sunlit) leaves in clear and overcast conditions were surprisingly similar given the differences in the amount of incident PAR above the canopy for those conditions. The main difference between overcast and clear conditions was found in the PAR received on the once-shaded leaves. The maximum PAR experienced by once-shaded and twice-shaded leaves in a rice canopy was estimated to be 177 and $18 \mu\text{mol m}^{-2} \text{s}^{-1}$ for clear conditions and 48 and $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for overcast conditions, respectively. Over that range, differences in the maximum rate of

individual leaf photosynthesis, and to a lesser extent quantum yield at low PAR, will determine the actual rate of leaf photosynthesis. At an irradiance (PAR) of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, the rate of leaf photosynthesis of rice is about $25 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and the rate for maize is up to double that value (Mitchell and Sheehy 2000).

Canopy architecture is important for canopy photosynthesis, but we have to take into account the effects of solar elevation, as well as whether the irradiance is direct or diffuse, before the magnitude of its importance can be calculated. Furthermore, canopy architecture and solar elevation result in leaves that are not light saturated even at the highest irradiances observed on clear days.

Relationship between leaf photosynthesis, canopy photosynthesis, and yield

Can leaves of C_3 plants photosynthesize at the same rates as those of C_4 plants? Evans and von Caemmerer (2000) showed that the maximum rate of leaf photosynthesis per unit leaf area for both C_3 and C_4 plants was a linear function of leaf N content; the slope of the relationship for C_4 s was greater than for C_3 s. At high leaf N contents, the maximum rate of individual leaf photosynthesis per unit leaf area in C_3 plants can be as high as that in C_4 plants with lower N contents. So, leaves of individual C_3 plants can have rates of photosynthesis comparable to those of C_4 leaves. Sheehy et al (1980) showed that, in a population of individually spaced alfalfa plants, maximum photosynthetic rates per unit leaf area varied from about 13 to $51 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$. In addition, there was a good relationship between whole-plant photosynthesis and plant N content, but there was no relationship between individual leaf photosynthesis per unit leaf area and whole-plant photosynthesis. Whole-plant photosynthesis depends on both the rate per unit leaf area and the total leaf area of the whole plant and these can be somewhat independent of each other. Pearce et al (1969) showed that leaf photosynthesis in alfalfa depended on specific leaf weight (dry weight of leaf for unit area), so small thick leaves could have much higher rates of photosynthesis than larger thinner leaves; specific leaf weight was shown to be largely governed by growing conditions. Therefore, it was not surprising that there was no relationship between individual leaf photosynthesis and whole-plant photosynthesis in the experiments of Sheehy et al (1980). Furthermore, the maximum rate of photosynthesis of successive youngest fully expanded leaves in grass canopies declined because they developed inside the canopy in increasingly shaded conditions (Sheehy 1977, Woledge 1973). The photosynthetic rate of leaves developing on plants grown as spaced individuals differs from the photosynthetic rate of leaves developing on plants growing in dense communities (Sheehy 2001b). As an interesting aside, in the experiments of Sheehy et al (1980), the rate of biological nitrogen fixation in alfalfa depended on whole-plant photosynthesis, which in turn depended on whole-plant N content.

In crops, leaves dilute their nitrogen, and consequently their photosynthetic machinery, as they reduce their specific leaf weight and expand their leaf area owing to competition for light (Sheehy 2001b, Lemaire et al 2007). Indeed, Greenwood et al (1990) showed that, for optimally fertilized C_3 and C_4 crops, the relationship between %N and plant dry matter per unit ground area had the same form; the relationship

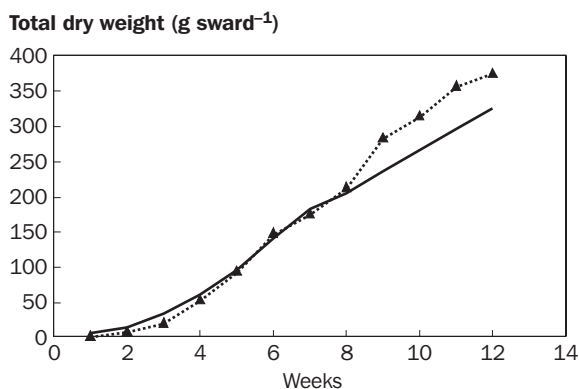


Fig. 7. The relationship between cumulative biomass production (▲) and cumulative measured canopy gross photosynthesis (—, hexose equivalent dry weight) in swards of perennial ryegrass (after Robson 1973).

declined with increasing biomass according to a power law. Under optimal supply of nitrogen, C_4 crops contained a lower concentration of N than C_3 crops at the same biomass, probably as a consequence of their higher rates of photosynthesis per unit of N.

Canopy and leaf photosynthesis were measured in grass canopies and the maximum rate of canopy photosynthesis per unit leaf area was correlated with the maximum rate of leaf photosynthesis per unit leaf area (Sheehy 1977). In those experiments, the relationship between canopy photosynthesis and irradiance was described using a simple hyperbolic relationship. In a more rigorous theoretical analysis of the relationship between canopy photosynthesis, leaf photosynthesis, and irradiance, Sheehy and Johnson (1988) showed that the maximum quantum yield of the grass crop depended on the fractional light interception, leaf transmissivity, and the maximum quantum yield of an individual leaf. They also showed that the maximum rate of canopy photosynthesis depended on LAI and the maximum rate of leaf photosynthesis. At a given temperature and concentration of atmospheric CO_2 , canopy photosynthesis is completely governed by irradiance, canopy architecture, and leaf photosynthesis. Robson (1973) showed a very close relationship between cumulative biomass production and cumulative measured canopy gross photosynthesis in swards of perennial ryegrass (Fig. 7). The relationship is not surprising because the carbon content of plants is approximately 40%. In conclusion, there are clear relationships between leaf photosynthesis, canopy photosynthesis, and biomass.

Leaf and canopy temperature

Long (1999a,b) predicted daily rates of canopy photosynthesis for C_3 and C_4 canopies and suggested that C_3 s have temperature optima close to 23 °C whereas rates for C_4 s were still increasing at 35 °C. Leaf temperature is influenced by meteorological

conditions as well as stomatal and boundary layer resistances. For a nontranspiring leaf, the energy balance equation can be written as

$$\rho c_p (T_d - T_a)/r_b = \alpha R_s - R_{dl} \quad (5)$$

where ρ is the density of the air, c_p is the specific heat capacity, T_d is the temperature of the nontranspiring leaf, T_a is the temperature of the air, r_b is the boundary layer resistance of the leaf, α is the fractional absorption of solar energy of a leaf, R_s is the irradiance of the leaf ($R_s = I_0(1 - s)$), and R_{dl} is the net emission of long-wave radiation by the leaf. By rearranging the equation, the difference between the temperature of a nontranspiring leaf and air temperature can be written as

$$T_d - T_a = r_b \alpha R_s / \rho c_p - r_b \alpha R_{dl} / \rho c_p \quad (6)$$

To evaluate the parameters of equation 6, leaves of the NPT were smeared with petroleum jelly to prevent transpiration. The temperatures of smeared and nonsmeared leaves were measured using an infrared thermometer. The difference between the temperature of the nontranspiring leaves and air temperature was plotted against the PAR incident on the leaves; the relationship was significant, albeit not impressively ($P < 0.01$; Fig. 8A). Assuming that the leaf is a black body ($\alpha = 1$) and using equation 6, the boundary layer resistance was calculated to be 53 s m^{-1} and R_{dl} to be 70 W m^{-2} ; both are reasonable values for crops (Woodward and Sheehy 1983, Monteith 1973). The energy balance for a transpiring leaf can be written as

$$\rho c_p (T_a - T_l)/r_b + (\alpha R_s - R_{wl}) = \lambda E \quad (7)$$

where T_l is the temperature of the transpiring leaf, R_{wl} is the net emission of long-wave radiation by the transpiring leaf, λ is the latent heat of vaporization, and E is the rate of transpiration. In theory, there is no simple relationship between leaf temperature and absorbed radiation, but in practice there was a very good correlation ($P < 0.001$; Fig. 8B). In addition, leaf temperature was less than air temperature ($T_l = 0.96T_a$; $P < 0.001$).

Ku et al (2000) suggested that, when the maize PEPC gene was inserted in rice, leaf conductance increased. It is interesting to ask, Would changing rice from being a C_3 to a C_4 have any effect on leaf temperature via altered leaf conductance? Clearly, this is not an easy question to answer in the absence of C_4 rice growing in the field. At the time of writing this paper, the best we could do to provide a clue was to compare photosynthesis, transpiration, and leaf temperatures in rice (IR72), a C_4 weed (*Echinochloa glabrescens*), and maize growing as well-watered individual plants in a screenhouse. Measurements made with a Licor 6400 showed that the rate of leaf photosynthesis of the C_4 leaves was approximately 29% greater than that of rice (Table 2). Conversely, the rate of leaf transpiration of the C_4 s was approximately 68% of the rate for rice and the value of leaf conductance for C_4 s was 45% of the value for rice. The temperature measurements showed that the C_4 leaves were warmer (33°C) than

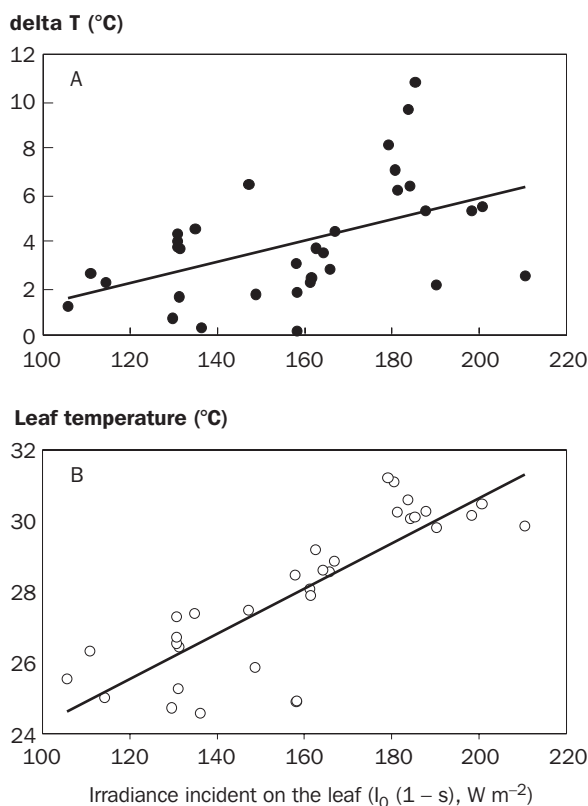


Fig. 8. (A) The relationship between the difference between leaf and air temperature and irradiance incident on the leaf for nontranspiring leaves of rice ($y = 0.045x - 3.17$, $r^2 = 0.24$). (B) The relationship between leaf temperature and irradiance incident on the transpiring leaf in rice ($y = 0.064x + 17.92$, $r^2 = 0.68$).

the C_3 leaves ($31^\circ C$), but both were less than air temperature ($34.5^\circ C$). The results suggest that leaf temperatures in rice could increase by about $2^\circ C$ as a consequence of changing the photosynthetic pathway from C_3 to C_4 . When transpiration was prevented by smearing the leaves with petroleum jelly, there were differences in the leaf temperatures (T_d) of the different species (Table 2). This suggested that the properties of the leaves (other than stomatal conductance) governing heat exchange were different. Those properties are probably associated with the absorption of radiation (Davies and Buttymor 1969) or boundary layer resistance or both.

The result of Ku et al (2000) suggested that C_4 rice leaves might be cooler than C_3 rice leaves. However, the comparison between rice and the C_4 species used here

Table 2. Measurements of gas exchange and leaf temperature made on the first fully expanded leaves of plants growing in well-watered pots in a screenhouse at IRRI. The PAR in the Licor 6400 chamber was 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and in the screenhouse was 1,140 $\mu\text{mol m}^{-2} \text{s}^{-1}$; the air temperature in the screenhouse was 34.5 °C. Leaves were coated with petroleum jelly to prevent transpiration. The standard errors are in parentheses, n = 6.

Item	C ₄ plants		C ₃ plants
	<i>Zea mays</i>	<i>E. glabrescens</i>	<i>O. sativa</i> (IR72)
Rate of photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	31.3 (0.05)	28.8 (0.61)	23.6 (2.20)
Stomatal conductance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.2 (0.01)	0.2 (0.01)	0.4 (0.00)
Rate of transpiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	4.1 (0.22)	3.9 (0.09)	5.9 (0.56)
Leaf temperature in Licor chamber (°C)	33.5 (0.20)	32.8 (0.30)	31.2 (0.20)
Leaf temperature in screenhouse (°C)	32.8 (0.10)	32.9 (0.10)	31.1 (0.10)
Temperature for leaves coated with petroleum jelly (°C)	39.1 (0.20)	37.3 (0.20)	35.4 (0.20)

suggests the opposite. The effect of C₄-ness on leaf and canopy temperature in rice remains unclear.

Radiation-use efficiency: two strategies for C₄ rice

Early theoretical work at IRRI suggested that grain yields of 15 t ha⁻¹ were possible. This suggestion rested on erroneous values for the efficiency of radiation conversion used by Yoshida (1981). The instantaneous value of the radiation conversion factor (or radiation-use efficiency), ϵ , expressed as g DW MJ⁻¹ (dry weight above ground, intercepted PAR in energy terms), can be written (Sheehy 2001a) as

$$\epsilon = \frac{0.64 P_g(t) - m_T W_s(t) - D_s(t)}{I_{\text{int}}} \quad (8)$$

where P_g is canopy gross photosynthesis (shoot net photosynthesis plus shoot respiration for the daylight hours), W_s is shoot weight and D_s is the rate of detachment of shoot weight, m_T is the maintenance respiration coefficient at temperature T , I_{int} is the daily total of intercepted PAR (MJ m⁻² d⁻¹), assuming that each variable has been measured for a day, and t is time. $D_s(t)$ is negligible during vegetative growth and so it can be seen that ϵ is strongly influenced by photosynthesis.

An experiment to compare yields and radiation-use efficiencies of rice, maize, and the C₄ weed *Echinochloa glabrescens* was conducted at IRRI in the dry season of 2006.

The crops were sown and transplanted so that they started to grow and intercept PAR at about the same time. All the crops received 340 kg N ha⁻¹, 50 kg P ha⁻¹, and 340 kg K ha⁻¹ and all of P and K fertilizers were applied as basal fertilizer incorporated a day before planting. For IR72 and maize, the N was split and applied weekly as follows: 60% at 14–50 DAT, 30% at 50–70 DAT, and 10% at 70–90 DAT. For *E. glabrescens*, the N was split and applied weekly as follows: 60% at 0–21 DAT and 40% at 21–50 DAT. The rice and weed were grown as irrigated crops (flood irrigation) and maize was irrigated every other day (i.e., grown in soil without surface water but kept well watered). Interception of PAR was measured twice weekly using a Delta T Sunscan probe and total aboveground biomass was measured weekly in the standard way (Sheehy et al 2004b, Cassman et al 1993). Both rice and maize were followed to maturity (rice, 98 days; maize, 101 days), whereas measurements ceased in *E. glabrescens* when the seeds started to shatter (42 days after transplanting). It can be seen in Figure 9A that the weed closed its canopy earlier than maize, and rice was the slowest to close. Monteith (1977) defined the slope of the relationship between shoot biomass and cumulative intercepted PAR as ϵ (Fig. 9B). In the above experiment, the values of ϵ were 4.4 g DW MJ⁻¹ for maize, 4.0 g DW MJ⁻¹ for *E. glabrescens*, and 2.9 g DW MJ⁻¹ for rice. At maturity, the total aboveground biomass of rice was 17.9 ± 0.38 t ha⁻¹ and that of maize, on the same day, was 28.8 ± 2.2 t ha⁻¹. The ratio of the values of ϵ were maize:rice 1.52 and *E. glabrescens*:rice 1.38. At 14% moisture content, the grain yield for maize was 13.9 ± 0.13 t ha⁻¹ and for rice was 8.3 ± 0.13 t ha⁻¹.

The ratios of the radiation-use efficiencies and the ratios of the grain yields for maize and rice strongly suggest that C₄ rice would be substantially more productive than C₃ rice. From these results, we suggest two strategies that could be adopted for the crop duration of C₄ rice: a maize-like duration (100 days) and a weed-like duration (50 days). With the maize-like duration, C₄ rice biomass would be 50% greater than C₃ rice biomass so the plants would have to be correspondingly larger. With the weed-like duration, the biomass of C₄ rice would be comparable with that of a 100-day-duration C₃ rice, but it would be achieved in about 60 days.

Is the sink in rice big enough for C₄ productivity?

Table 3 shows the number of juvenile spikelets 10–15 days before panicle emergence, the number of spikelets at maturity, and the number of filled spikelets (grains) measured for IR72 in two dry seasons (Sheehy et al 2001). It can be seen that the capacity of rice crops for spikelet production (more than 100,000 m⁻²) is more than double the final number of grains at maturity (less than 50,000 m⁻²). Increased photosynthesis for 33 days prior to heading as a consequence of carbon dioxide enrichment was the probable cause of the 30% increase in grain yields observed by Yoshida (1973). In his experiments, the treatment increased mature spikelet number and the improved yield was the result of an increased filling percentage and individual grain weight.

The sink is much larger than required for C₃ rice and the evidence suggests that another 50% of the juvenile spikelets could be converted into grains in C₄ rice.

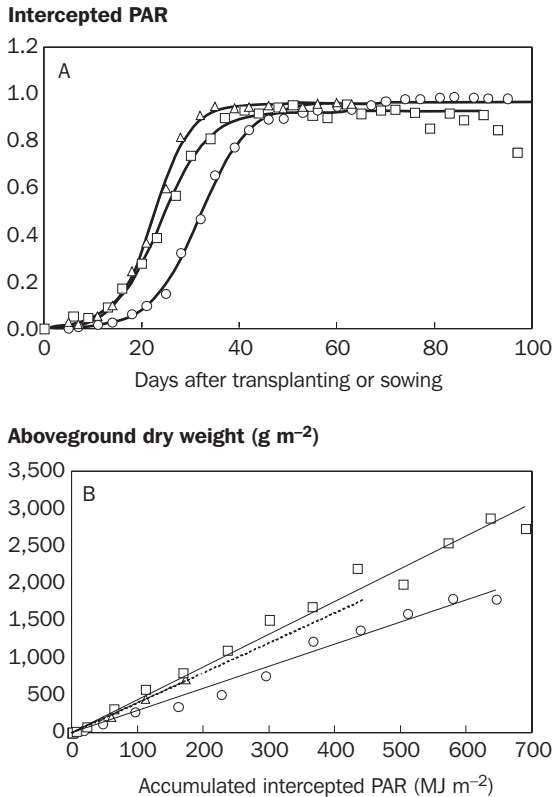


Fig. 9. (A) The time courses of fractional intercepted PAR during crop growth following transplanting (rice (IR72), \circ ; *Echinochloa glabrescens*, Δ) or sowing (maize, \square). The fitted curves are of the form $y = a/(1 + \exp(-(x - b)/c))$ and are used simply to highlight the differences; note that interception in maize declined after day 90. (B) The relationship between accumulated intercepted PAR (MJ m⁻²) and aboveground dry weight for rice (IR72), *Echinochloa glabrescens*, and maize; symbols as in (A).

Searching for C₄-ness in wild rice

Rice belongs to the tribe *Oryzeae*, which consists of 12 genera (Vaughan 1994). The genus *Oryza* contains 24 species, two are cultivated and the others are “wild” rice; there are about 6,000 wild rice accessions in the IRRI germplasm collection. The wild types have not been studied in detail, but past work has suggested that some of the wild types have intermediate C₃-C₄ characteristics. Some accessions of *O. rufipogon* were reported to have CO₂ compensation points of about 30 $\mu\text{mol mol}^{-1}$ and PEP carboxylase activity of about 3 $\mu\text{mol min}^{-1} \text{mg}^{-1}$ chlorophyll (Yeo et al 1994). Furthermore, those authors observed that the photorespiration rates of *O. rufipogon*

Table 3. The mean number of juvenile spikelets, spikelets at maturity, filled spikelets, and 1,000-grain weight in crops of IR72 in the dry seasons of 1997 and 1999.

Item	Mean number
Number of juvenile spikelets (m ⁻²)	113,848
Spikelets at maturity (m ⁻²)	51,372
Filled spikelets at maturity (m ⁻²)	38,793
1,000-grain wt. (g, 14% moisture content)	24.0

Source: Sheehy et al (2001).

were 25% lower than the rates of *O. sativa*. In addition, there is evidence for some C₄ characteristics in rice spikelets (Imaizumi et al 1997). The conclusion of those authors was that the lemmas carried out mainly C₃ photosynthesis, but also fixed some carbon dioxide by PEPcase, a mixture of routes not typically C₃ or C₄ but perhaps adapted to re-fix abundant carbon dioxide from respiration; Kranz anatomy was lacking. As a preliminary investigation, it was decided to screen a representative sample of 130 accessions drawn from the 6,000 wild relatives of rice (WRS) for aspects of anatomy and physiology associated with C₄ness. A representative from each species in the IRRI collection was included in the subsample. A small collection of C₄ plants was used to characterize some of the attributes of their leaves: *Digitaria ciliaris*, *Echinochloa colona*, *E. crus-galli*, *E. glabrescens*, another species of *Echinochloa* identified to genus only, *Panicum maximum*, and *Rottboellia cochinchinensis*.

C₄ plants discriminate less than C₃ plants against the heavier isotope ¹³C, and the ratio of ¹³C to ¹²C ($\delta^{13}\text{C}$) is used to identify plants with a C₄ pathway (Cerling 1999). The $\delta^{13}\text{C}$ values for the WRS ranged from -32‰ to -25.1‰ and showed there were no C₄ types in the subsample (Fig. 10). The number of veins in a youngest fully expanded leaf (N_v) was significantly correlated with leaf width (L_w). In C₄ leaves, the relationship was $N_v = 11 L_w$ ($P < 0.001$, leaf width in mm) and in WRS leaves it was $N_v = 5 L_w$ ($P < 0.001$); C₄ leaves contain twice as many veins per unit leaf width than C₃ leaves. The interveinal spacing (at the middle of the blade) for the WRS ranged from 113 to 322 μm (the value for IR72 was 170 μm). The range for the C₄ weeds was 93 to 136 μm . Currently, mesophyll cell size is being estimated for the subsample and C₄ weeds. The total number of bundle sheath cells (BSC) and the number containing chloroplasts in small veins were counted. The percentage of the BSC containing chloroplasts and the percentage of BSC plan area occupied by chloroplasts were estimated; Table 4 shows some of the values for selected species. Interestingly, 100% of the BSC contained chloroplasts in *O. longistaminata* and 48% of its plan area was occupied by chloroplasts; in the C₄ species, more than 80% of the BSC plan area was occupied.

Wild rice types probably have some of the anatomical features peculiar to C₄ plants and the wild types may contain C₃-C₄ intermediates. In 2007, an enclosure technique for mass screening rice seedlings will be developed and the whole wild rice collection will be screened for photosynthetic efficiency.

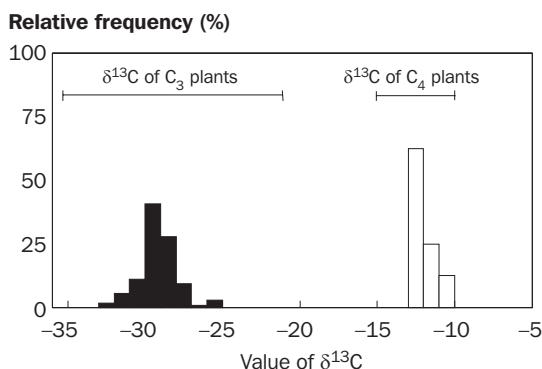


Fig. 10. Distribution of $\delta^{13}\text{C}$ values of the representative subsample of wild rice (■) and a small collection of C_4 plants (□). The range of $\delta^{13}\text{C}$ values for C_3 and C_4 plants shown is from Cerling (1999).

Table 4. Percentage of bundle sheath cells (BSC) containing chloroplasts in small vascular bundles and percentage of BSC plan area apparently occupied by chloroplasts, determined using confocal microscopy.

Species	Source	BSC with chloroplast (%)	Chloroplast area in the BSC (%)
C_4	Our collection	100	>80
C_3	Cultivated rice		
	<i>Oryza sativa</i> (IR64)	100	21
	Some wild rice		
	<i>O. alta</i>	50	52
	<i>O. australiensis</i>	88	41
	<i>O. barthii</i>	64	41
	<i>O. longistaminata</i>	100	48
$\text{C}_3\text{-C}_4$	<i>Panicum milioides</i>	100	50

Conclusions

The reason for converting the photosynthetic system in rice from C_3 to C_4 is necessity rather than curiosity. It is not good enough to be optimistic that “business as usual” will solve the problem of increasing future rice yields. New and possibly radical approaches need to be explored urgently. Using fuel more efficiently in a car with a nearly emissions-free engine is undoubtedly part of the future of motoring. Large sums of money have been invested, and the hybrid engines and fuel cells of today represent the legacy of yesterday’s research. Using sunlight, land, water, and other resources more efficiently to produce food is an even greater imperative in the face of increasing populations, climate change, and economic uncertainties of the future. Can

there really be any doubt that research aimed at providing the very best engine for the rice plant should be the highest priority of the International Rice Research Institute? Evolution has invented such an engine (C_4 photosynthesis) and we need to install it in the world's most important food crop.

It will take an international consortium of research institutions to make this a reality over the next 10 to 15 years. To that end, IRRI formed a C_4 Rice Consortium involving scientists from both advanced institutions and the developing countries. The Consortium will chart and conduct the research needed to invent C_4 rice and will seek financial support from donors.

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Notes

Authors' addresses: J.E. Sheehy, A.B. Ferrer, A. Elmido-Mabilangan, P. Pablico, and M.J.A. Dionora, Crop and Environmental Sciences Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines, e-mail: j.sheehy@cgiar.org; P.L. Mitchell, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.

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The case for C₄ rice

P.L. Mitchell and J.E. Sheehy

The case for C₄ rice is summarized as a chain of argument, starting from the need to produce more rice, through higher yield potential, to the consequent improvements in growth and photosynthesis. We conclude that it is essential to make Rubisco, the key enzyme of photosynthesis, work harder, by concentrating carbon dioxide around Rubisco, thus raising the light-saturated rate of photosynthesis and greatly reducing photorespiration, as occurs in C₄ photosynthesis. The additional agricultural benefits of shifting from C₃ to C₄ rice are that C₄ photosynthesis requires (1) less Rubisco and hence less nitrogen, and (2) less water, since a steeper concentration gradient for carbon dioxide diffusion can be maintained through partly closed stomata.

The chain of argument also shows that research should be planned from the perspective of what we wish to achieve, that is, from the top downward, and quantitatively as far as possible. Developments in screening phenotypes, plant breeding, molecular biology, and genetic engineering are proceeding rapidly and need to be directed toward the applied goal. The pathway to success cannot be seen completely but it is very likely that techniques will arise to enable the construction of C₄ rice. The certainties of population growth, climate change, and future shortages of water for agriculture mean that it is essential to start research now.

Keywords: C₄ photosynthesis, C₄ rice, Rubisco, top-down planning, yield potential

We started thinking seriously about C₄ rice in 1998, and we were far from being the first (see Burnell, this volume; Akita 1994). Three pieces of information were influential (Mitchell et al 1998).

1. Crop biomass and yield are directly proportional to the solar radiation intercepted by the crop (Monteith 1977) and the constant of proportionality, a measure of how effectively radiation is converted to energy in biomass, is the radiation conversion factor, so-called radiation-use efficiency (RUE).
2. There is a consistent large difference in RUE between C₄ maize and C₃ rice.

3. Ultimately, RUE depends on the surplus of photosynthesis over respiration; little can be done to decrease respiration so higher RUE, biomass, and yield require increased photosynthesis.

Evidence is also accumulating to show that the C_4 mechanism is added to the basic system of C_3 photosynthesis, and has been added by evolution on many occasions (Mitchell and Sheehy 2006); nonetheless, C_4 rice has not evolved naturally so making it is an ambitious project. For nearly a decade, the idea has continued to seem attractive to us, almost inevitable for a substantial gain in rice productivity, and we have refined our arguments for C_4 rice. There are two parts to the case. The first is a chain of argument leading from the need to reduce hunger and poverty (Millennium Development Goals—IRRI 2006), through an increase in rice productivity, the need for a substantial increase in yield potential, and a corresponding increase in photosynthesis, to the features of C_4 photosynthesis that appear so advantageous. The second part is the rapid progress made in screening methods for desirable phenotypes, plant breeding with biotechnology, molecular biology, and genetic engineering. The chain of argument would remain as armchair speculation if it were not for the astonishing rates of progress in these fields.

The chain of argument

Most of the justification for the chain of argument, set out in Table 1, can be found in Dawe (2000), Sheehy (2000), and Mitchell and Sheehy (2000); it is also summarized in Mitchell and Sheehy (2006). A completely independent analysis by Long et al (2006) for grain crops reaches the same conclusion: that improved photosynthesis is necessary to increase yields, and they explore several methods for this, overlapping with ideas in Table 1. We will comment briefly on a few links in the chain.

For Requirement 5, there are several reasons for selecting a 50% increase in yield potential. First, yield potential in rice (tropical, growth duration around 110 days) has stagnated for 30 years at about 10 t ha^{-1} (Cassman et al 2003); it is time to catch up. Second, rice yields of 15 t ha^{-1} do occur in temperate regions with growth durations of 5–6 months (IRRI 2002) so rice culms (stems) can be strong enough for panicles that are 50% heavier (assuming the same number of culms per unit area). Third, the RUE of maize, a typical productive C_4 plant, is 50% greater than that of rice (Mitchell and Sheehy 2000), recently confirmed by experiments at IRRI (Sheehy et al, this volume).

An alternative method of raising yield potential (Requirement 5) would be to take a smaller yield from each of two crops of shorter duration, for example, 7.5 t ha^{-1} in 50 days, both fitted into the tropical dry season when solar radiation is the highest in the year. This is prompted by the observation (Sheehy et al, this volume) that the rapid growth of the C_4 weed *Echinochloa glabrescens*, RUE 38% higher than rice, was channeled into a much shorter growth duration: 42 days from transplanting of seedlings to seed dispersal. A very short duration rice of this high productivity ($150 \text{ kg ha}^{-1} \text{ day}^{-1}$) would also permit more diverse cropping patterns, which could include

Table 1. The chain of argument leading to C₄ rice. Abbreviations are given at the end of the table.

Requirement	Reasons
1. Alleviation of hunger and poverty in global regions dependent on rice	Simple humanity; contribution to Millennium Development Goals and to the missions of IRRI and the CGIAR.
2. Rice crops	Rice, rather than other crops, for cultural, nutritional, and agro-climatic preferences.
3. Increased productivity of rice crops	Provides several routes to alleviation of poverty through lower price of rice, higher profits for farmers, increased demand for agricultural labor.
4. Increase in yield per hectare	From increased productivity, and because suitable arable area in rice regions is decreasing slowly but steadily.
5. Increase yield potential of new cultivars by 50%	To increase yields while maintaining yield gap between yield potential and farm yields. Increase from 10 t ha ⁻¹ to 15 t ha ⁻¹ for which rice culms are strong enough (110-day growth duration, yield from 90 to 135 kg ha ⁻¹ day ⁻¹). Or a yield of 7.5 t ha ⁻¹ over a duration of 50 days (150 kg ha ⁻¹ day ⁻¹), to fit two crops into the dry season with high solar radiation.
6. Increase crop biomass by 50%	Cannot increase harvest index beyond 0.5, which is the best currently obtainable.
7. Increase in number of spikelets filled by 50%	Many more spikelets are initiated on the panicle than appear as filled grains so there is unused capacity for yield.
8. Increase RUE by 50%	Crop growth is driven by intercepted PAR, and cannot increase crop duration, incident PAR, or fraction of PAR intercepted.
9. Increase canopy photosynthesis by 50%	Daily RUE is balance of photosynthesis and respiration, and there are no obvious ways of reducing respiration.
10. Increase in leaf photosynthesis	To contribute to canopy photosynthesis.
11. Higher rate of leaf photosynthesis when saturated by PAR	For leaves in the canopy receiving high PAR, i.e., high in the canopy, at appropriate angles, when incident PAR is high.
12. Higher quantum yield	For leaves in the canopy receiving low PAR, i.e., in canopies with PAR well distributed through the canopy, or when incident PAR is low.
13. Better performance from Rubisco	No alternative to Rubisco for continuous net fixation of carbon dioxide into carbohydrate, but suffers from oxygenation activity, hence occurrence of photorespiration.

Continued on next page

Table 1 continued.

Requirement	Reasons
Options	
(a) More Rubisco in thicker leaves	More photosynthesis from more Rubisco (but requires more nitrogen).
(b) Better Rubisco: higher specificity for carbon dioxide	Reduced photorespiration (but also brings lower rate of catalytic activity so may not increase rate of leaf photosynthesis by much).
(c) Protect Rubisco from oxygen: confine to chloroplasts without PSII	Reduced photorespiration (but not necessarily a large increase in rate of leaf photosynthesis).
(d) Make Rubisco work harder by increasing concentration of carbon dioxide around Rubisco	Absence of photorespiration and more effective use of Rubisco in higher concentration of carbon dioxide.
14. From 13, option (d): C_4 photosynthesis as productive as maize	Maize RUE 50% higher than rice RUE; both maximum rate of leaf photosynthesis and quantum yield higher than in rice. Better use of nitrogen and water.
15. Features of C_4 photosynthesis in maize	
I. Concentration of carbon dioxide around Rubisco raised 3–8 times higher than in C_3 plants	Raises maximum rate of leaf photosynthesis.
II. Low leakage from the compartment with Rubisco, by low conductance for carbon dioxide	Minimizes futile cycling and minimizes reduction in quantum yield from leakage.
Options	
(a) C_4 photosynthesis with Kranz anatomy	By far the commonest C_4 system, high productivity in many cases (maize, sugar cane, <i>Miscanthus</i>).
(b) Single-cell C_4 photosynthesis with low leakage	Avoids complexity of anatomical modification; requires changes within existing photosynthetic cells only; allows design of systems not occurring naturally.
16. From 15, option (a): C_4 photosynthesis with Kranz anatomy, as in maize	
I. Kranz anatomy	Spatial separation of initial fixation in mesophyll cells from final fixation in bundle sheath cells but connection by abundant plasmodesmata for rapid diffusion of metabolites. Reduction in leakage of carbon dioxide from bundle sheath cells to maintain high concentration around Rubisco. Close vein spacing so each mesophyll cell is adjacent to a bundle sheath cell.

Continued on next page

Table 1 continued.

Requirement	Reasons
II. Changed pattern of expression of photosynthetic enzymes	In mesophyll cells, need PEPcase of C ₄ type in large amounts, and CA and PPK. In bundle sheath cells, need NADP-ME (or other decarboxylating enzyme) and Rubisco, absence of CA, absence of PSII. Appropriate changes to transporters across the chloroplast envelope.
17. From 15, option (b): single-cell C ₄ photosynthesis with low leakage	
I. Chloroplast envelope with reduced conductance to carbon dioxide	Need to reduce leakage from the compartment in which carbon dioxide concentration is raised to minimize futile cycling and maximize quantum yield.
II. Changed pattern of expression of photosynthetic enzymes	In cytosol, need PEPcase of C ₄ type in large amounts, and CA and PPK (if carboxylase is NADP-ME). In chloroplast, need decarboxylase (NADP-ME or PEPCK), absence of CA. Appropriate changes to transporters across the chloroplast envelope.

Abbreviations in Table 1: CA = carbonic anhydrase, CGIAR = Consultative Group on International Agricultural Research, NADP-ME = NADP-dependent malic enzyme, PAR = photosynthetically active radiation, PEPcase = phosphoenolpyruvate carboxylase, PEPCK = phosphoenolpyruvate carboxykinase, PPK = pyruvate, orthophosphate dikinase, PSII = photosystem II, Rubisco = ribulose 1,5-bisphosphate carboxylase-oxygenase, RUE = radiation-use efficiency.

extra vegetable crops or crops for biofuel, addressing the alleviation of hunger and poverty (Requirement 1) in other ways.

Requirement 7 tackles the problem of matching source and sink in the formation of grain yield. Sheehy et al (2001) showed that many more spikelets (florets) are initiated on the panicle than appear as filled grains, that is, there is spare capacity in the sink, which can use photosynthate from a larger source.

The key role of Rubisco (Requirement 13) arises from its being the only carboxylase to provide a continuous net gain in fixed carbon, given biochemistry based on carbohydrate, particularly trioses, pentoses, and hexoses. Rubisco can be made to work harder (Option d of Requirement 13) by providing it with conditions more like the primitive atmosphere in which it evolved, an atmosphere higher in carbon dioxide and much lower in oxygen. Experiments with elevated concentrations of carbon dioxide show that Rubisco in rice can indeed respond with increased photosynthesis (Baker and Allen 1993, Ziska et al 1997, Kobayashi et al 2005). The objective of constructing C₄ rice is to make the plant itself provide a higher concentration of carbon dioxide around Rubisco; in C₄ plants, this concentration is 3–8 times higher than in C₃ plants (Requirement 15, I; Kanai and Edwards 1999).

Requirement 15, II refers to the sensitivity of quantum yield in C₄ plants to leakage from the compartment in which carbon dioxide concentration is raised (bundle sheath cells in Kranz anatomy, chloroplasts in single-cell C₄). When carbon dioxide

is lost from this compartment, the energy required to regenerate phosphoenolpyruvate (PEP) from pyruvate has been used in vain (since carbon dioxide has been fixed and then re-appears after decarboxylation—futile cycling). The advantage in quantum yield that C_4 plants have over C_3 plants is because the absence of photorespiration outweighs the cost of regenerating PEP (at temperatures above 21 °C) but the advantage is easily squandered if leakage is high (Mitchell and Sheehy 2000).

Requirements 16 and 17 sketch the pathways to C_4 rice, with or without Kranz anatomy, respectively.

We have focused on the route to C_4 photosynthesis in Table 1 but there are branching points from the chain. For example, from Requirement 8, in principle it could be worth lengthening the growth duration of the wet-season crop in the humid tropics when only one crop is to be taken, to make better use of a growing season of 7 months. Possibly there are changes in the timing of canopy growth and in canopy architecture that could produce improved canopy photosynthesis that would lead to higher yields (Requirement 9). Option b in Requirement 13 has been explored by Zhu et al (2004), as summarized in Mitchell (this volume). Accepting the inevitable oxygenase activity of Rubisco but arranging that the photorespiratory mechanism releases carbon dioxide in the chloroplast, for recapture by Rubisco, has been tried by Peterhänsel et al (this volume). Long et al (2006) make several suggestions, some mentioned above (canopy architecture) or in Table 1 (better Rubisco), but in addition a better rate of recovery from photoprotection so that leaves experiencing a decrease in light below saturation resume photosynthesis more rapidly, or faster regeneration of ribulose 1,5-bisphosphate (RuBP) to increase rates of light-saturated photosynthesis. Raines (2006) also discusses some of these possible improvements to photosynthesis, and others such as improving the heat stability of Rubisco activase above 30 °C, or using a cyanobacterial enzyme for the accumulation of inorganic carbon, introduced into tobacco and *Arabidopsis* with some encouraging results although the precise function of the enzyme is unknown.

Any or several of these methods may be effective in increasing rice photosynthesis, perhaps in the range of 10–25%. But only C_4 photosynthesis offers the prospect of a substantial increase of 50% plus more effective use of nitrogen and water (summarized in Mitchell and Sheehy 2006). Although significant amounts of enzymes in the C_4 pathway are required, they are more than offset by the decreased amount of Rubisco in C_4 plants so that overall the requirement for nitrogen is smaller (Greenwood et al 1990). The combination of carbonic anhydrase and PEP carboxylase in the mesophyll cells of C_4 plants takes up carbon dioxide very effectively, producing a low concentration in the air spaces of the leaf. This steepens the concentration gradient so that a rapid flux of carbon dioxide can be maintained even with a smaller stomatal conductance (reduced aperture), thus reducing transpiration. This will be a direct benefit to upland rice and to rainfed rice when the soil is dry. For irrigated rice, for which most water is used for soil preparation and flood irrigation, the increased yield per hectare will ensure higher water productivity for the crop.

Progress in techniques

Improvements in screening for phenotypes and modern plant breeding using biotechnology are covered by Hervé (this volume) and by Virk and Peng (this volume). What we have noted with interest, as nonpractitioners, is the progress in molecular biology and genetic engineering that appears relevant to the task of making C_4 rice. It is now routine to insert genes for C_4 photosynthetic enzymes into a C_3 plant and have them expressed successfully (Häusler et al 2002). The rice genome and most of the maize genome have been sequenced and are being annotated (Bruskiewich and Wanchana, this volume). There is increasing use of specific promoters so that genes are switched on only in particular tissues, or in response to environmental cues, or at particular stages of plant development. Many enhancer trap lines have been identified in rice (Wu et al 2003, Johnson et al 2005, Liang et al 2006) and these can be used for analysis of the genome since it is possible to control where in a plant the transgene is expressed. Plastids are being transformed, that is, genes can be inserted into the chloroplast and be expressed there (Maliga 2002, Lee et al 2006). We conclude that genetic engineering will provide a method for introducing C_4 photosynthesis into C_3 plants once the key genes are identified, not immediately but in the medium-term future.

As an example of the rate of progress, consider the speculation in August 2005 of one of us (P.L.M.), unhindered by expertise in this field, on possible methods of keeping together several genes introduced to rice by genetic engineering. “Perhaps the necessary genes could be inserted into the chromosome together so that segregation is minimized. In the future, will it be possible to introduce genes to particular positions in a selected chromosome? Are there genes that prevent crossover, perhaps of specific chromosomes? Could the genes be introduced on two small extra chromosomes, which pair and segregate but do not cross over, as sex chromosomes do?” In less than 18 months, we learned (Hervé, this volume) that several of these suggestions are already in use (site-specific recombination technology, chromosome-based engineering, artificial chromosomes).

The top-down approach

The top-down approach is appropriate for any complex task, certainly for one as difficult as constructing C_4 rice. It is essential to specify the final objective and work backward to plan the stages required to reach the objective. However, research so far on producing C_4 rice seems to have been pushed by technology: it is possible to introduce genes for a few enzymes of the C_4 pathway, thought to increase the rate of photosynthesis, so it has been tried (e.g., Ku et al 1999). This tendency seems to be common where genetic engineering is applied to crops. Sinclair et al (2004) pointed out that the weakness of this approach is that improvements made at the molecular level are dissipated when scaled up through biochemical and physiological levels to the response of crops in the field. In their calculations for soya bean, a 50% increase in messenger RNA for Rubisco declined to a 33% increase in maximum rate of leaf photosynthesis, then to an 18% increase in crop biomass, and finally to a 6% increase

in grain yield. The impetus for this kind of research generally comes from a newly developed technique in genetic engineering, so from the bottom, with the hope that the improvement will be worthwhile when scaled up.

In contrast, to construct C_4 rice will require a top-down approach, specifying the ultimate objective and then the steps required to achieve it, as in Table 1. The pathway to C_4 rice may not be short and direct: there are likely to be some surprises along the way, and additional refinements found to be necessary once the C_4 mechanism is introduced into rice. Some of these have been alluded to, such as the mechanical strength of culms and crop duration. The top-down approach also encourages a quantitative view since a numerical requirement at one step has implications for the next step down. For example, we need to state a desired and quantified improvement in yield potential, and then specify the changes in photosynthesis required. This then leads to seeking the solutions in terms of biochemistry, or biochemistry and anatomy, either in natural variation or in the genetic engineering required, or very likely both. Of course, to elaborate and quantify all the steps there is much work to be done, which will include mathematical modeling, experiments, and fieldwork, and probably comparative work on other species such as C_4 weeds of rice.

Envoi

It is easy to suggest that the construction of C_4 rice will be especially difficult given current knowledge, or that the cost might be unusually high for agricultural research. But the need is correspondingly high: global population continues to increase, climate change will alter cropping patterns and probably reduce yields, and water available for agriculture will become scarce or more expensive (IRRI 2006). The chain of argument (Table 1) leads us to the inescapable conclusion that we must make C_4 rice in order to achieve a 50% increase in yield potential while using nitrogen and water more efficiently. Constructing C_4 rice is a high-reward, high-risk venture, likely to take at least 15 years to complete. It will require the ingenuity and skills of researchers from around the world, hence the formation of a Consortium for C_4 Rice. We must start now, confident that developments in plant breeding, including genetic engineering, will provide the techniques required.

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Notes

Authors' addresses: P.L. Mitchell, Department of Animal and Plant Sciences, University of Sheffield S10 2TN, U.K.; J.E. Sheehy, Crop and Environmental Sciences Division, International Rice Research Institute, Los Baños, Philippines.

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Agricultural research, poverty alleviation, and key trends in Asia's rice economy

D. Dawe

Rice is the most widely planted crop in Asia and it is the dominant source of calories for Asians living in poverty. Since a majority of the world's poor live in Asia, improving the livelihoods of rice farmers and consumers is therefore critical to global poverty alleviation. Poor farmers need high profits from growing rice, and poor consumers need lower prices so that they can increase the quality and quantity of food consumption and still have money left over for investments in education. Agricultural research is perhaps the most important way to achieve both high profits for farmers and low prices for consumers.

Although some trends in the rice economy give cause for optimism regarding the future path of rice prices, other trends raise concerns that prices will increase in the next 20 years. Uncertainties abound regarding future oil prices, demand for biofuels, water scarcity, climate change, and the pace of slowdowns in population growth and dietary diversification. In the face of such uncertainty, it seems prudent to invest in research for C_4 rice. Without such investments in productivity-enhancing technologies, it is the poor who will suffer the most from adverse shocks that put upward pressure on food prices.

Keywords: rice, agricultural research, poverty alleviation

Rice is by far the most widely planted crop in the developing world, with average harvested area of 147 million hectares from 2003 to 2005 (wheat and maize were next, each with slightly less than 100 million hectares). It is also the most important source of calories for consumers in the developing world, providing 655 calories per capita per day, or 25% of total intake in 2003. Wheat is next, at 17% (all data in this paragraph are from FAO 2006a).

Although rice production and consumption are growing rapidly in Africa (from a small base), approximately 90% of the world's rice is produced and consumed in a belt ranging from Pakistan in the west to Japan in the east. This part of Asia, which will be referred to in this paper as rice-producing Asia (RPA), is also home to a majority of the world's poor. In 2001, more than 700 million Asians still lived on less than US\$1 a day, more than the entire population of sub-Saharan Africa at that time (FAO 2006b). To some extent, this is because Asia already has such a large population.

But even in relative terms, malnutrition appears to affect a substantially larger share of the population in South Asia than in Africa, the two poorest regions in the world (Svedberg 1999). As of 2000-02, there were still 548 million undernourished people in the developing and transition economies of Asia and the Pacific (FAO 2006b).

Rice is by far the most important commodity for the Asian poor. In many of the poorest countries, it accounts for more than 60% of caloric intake and more than half of protein consumption (Bangladesh, Cambodia, Lao PDR, Myanmar, and Vietnam), and it is usually more than 50% of the crop area harvested in those countries (all data are from FAO 2006a). For Asia and the Pacific as a whole, it accounted for 23% of total crop area harvested in 2004 (more than any other crop) and more than 30% of total caloric intake among Asian developing countries. In fact, while the countries of South, Southeast, and East Asia are very diverse in terms of religion, political structure, and stage of economic development, they are all united by the importance of rice in food, agriculture, and culture.

Given the dominant role of rice in the lives of Asia's poor, and the fact that most of the world's poor reside in Asia, rice research has the potential to make an important contribution to global poverty alleviation.

Pathways from agricultural research to poverty alleviation: theory¹

Direct, short-term benefits

How does rice research help alleviate poverty? In some ways, this is an easy question to answer. Higher standards of living for rice farmers can be sustained only if farmers are able to produce more rice per unit of input. This higher productivity leads to higher profits from farming and a reduction in poverty. Thus, one way that rice research helps alleviate poverty is by increasing the productivity of farmers. This is the "direct" contribution to poverty alleviation. It is an important one, and it applies primarily to farmers that own land. This short-term effect can also lead to longer-term effects, as farmers with increased profits invest in education for their children, helping to keep subsequent generations out of poverty.

Indirect, medium-term benefits

If this direct contribution were the only one, research priorities would be relatively simple to set. The only goal would be to help the poorest farmers directly, and this would mean working with farmers on marginal lands without access to roads and irrigation. But rice research also makes an important indirect contribution to poverty alleviation, a contribution that is often overlooked. This indirect contribution makes itself felt in both the medium term and the long term through lower prices that are the natural outcome of the law of supply and demand: increases in production reduce prices relative to what they would have been without the increase in production.

¹Parts of this section draw heavily on Dawe (2000).

Low prices are important because several classes of poor people do not have surplus rice to sell, and must buy their rice on markets. Such people often do not get enough to eat. In fact, the World Health Organization (WHO) in a recent issue of its World Health Report (2002) identified “being underweight” as the most burdensome health risk in the world, being responsible for the annual loss of 138 million disability-adjusted life years (DALYs). Lower food prices can contribute to reducing the incidence of underweight by increasing the affordability of food for the poor. Lower prices for basic foodstuffs also increase the effective income that the poor have at their disposal for other important expenditures such as education, health, and consumption of nutritious foods such as fish, meat, and dairy products.

Who are the poor people who are net consumers of rice? One increasingly important group is the urban poor. As of 2005, urban dwellers accounted for 38% of the total population in the developing countries of rice-producing Asia (RPA). Although this means that most of the population still lives in rural areas, urbanization is increasing. From 2000 to 2005, Asia’s rural population grew at just 0.26% per annum, while the urban population grew more than ten times as fast at 2.73% per annum. In absolute terms, the urban population increased by 167 million people from 2000 to 2005, whereas the rural population increased by just 29 million. Population projections indicate that the rural population will be declining in absolute terms before 2015, and the urban population will equal the rural population in RPA by 2025 (all data from UN 2006). Average levels of income are surely higher in urban areas than in rural areas, but not all urban dwellers are well-to-do. There is little doubt that, while there is more poverty in rural areas, the number of urban poor is increasing, both in absolute terms and as a share of the total (Haddad et al 1999).

A second important group of poor rice consumers is the rural landless or near landless who derive most of their income from agricultural labor. Landless agricultural workers are most common in South Asia, Indonesia, and the Philippines. They are less common in Thailand (where population density is lower), China, and Vietnam (due to comprehensive land reforms). In the Philippines, they constitute 13% of the agricultural labor force, and are one of the poorest groups in the countryside, with income 30% lower than that of rice farmers (Dawe et al 2006). Although some of these laborers work on rice farms and are occasionally paid in rice, surveys show that they do not earn enough rice to sell a surplus on the market. Instead, they need to purchase rice on markets and are likely to benefit from lower prices.

A third important group of poor rice consumers is rural dwellers who own land, but use it to grow nonrice crops. They would benefit from cheaper rice prices. In Indonesia, many farmers plant maize, cassava, and soybeans. In the Philippines, maize and coconut are important crops grown by poor smallholders, with maize farmers being particularly poor.

Thus, many poor Asians are net purchasers of rice. Rice constitutes an important part of their daily expenditures, so the contribution of lower prices is not trivial. For example, for the poorest 10% of the urban population in Bangladesh, rice accounts for half of total expenditures. Even for the poorest 60% of the urban population, nearly 40% of expenditures go to rice (Bangladesh Bureau of Statistics 1998). In Indonesia,

rice accounts for 20% of total expenditures for the poorest quarter of the urban population (about 20 million people). For the poorest 5% of the urban population, the share of rice is about 25% (Biro Pusat Statistik 1998).

What are the effects of high rice prices for those who spend a substantial proportion of their income on rice? Senauer and Sur (2001) estimated that, if there were a 20% increase in food prices between then and 2025 (due, for example, to a decline in funding for international rice research), the number of undernourished people in Asia would increase by 158 million. An interesting study using data from rural Central Java in Indonesia (Block et al 2004) found that, when rice prices increased in the late 1990s, mothers in poor families responded by reducing their caloric intake in order to better feed their children, leading to an increase in maternal wasting. Furthermore, purchases of more nutritious foods were reduced in order to afford the more expensive rice. This led to a measurable decline in blood haemoglobin levels in young children (and in their mothers), increasing the probability of developmental damage. A negative correlation between rice prices and nutritional status has also been observed in Bangladesh (Torlesse et al 2003).

Indirect, long-term benefits

While the short- and medium-term effects described above are important, poverty alleviation is ultimately a long-term, broad-based process, and higher farm productivity makes several important long-term indirect contributions to poverty alleviation. These effects operate through lower rice prices.

One pathway is that lower rice prices lead to increased calorie consumption and improved nutrition for the poor. Lower retail prices allow some people to consume larger quantities of rice (especially the very poor who are calorie-deficient), while also allowing people to spend less money on rice, which in turn frees up income to spend on other, more nutritious foods that can reduce “hidden hunger” by increasing the intake of important vitamins and minerals (Welch and Graham 1999). There is some evidence that increased calorie consumption increases the efficiency and productivity of laborers, especially those who work in jobs requiring physical strength (Strauss and Thomas 1998). Improved nutritional status can increase cognitive abilities (e.g., through increased consumption of iron-rich foods, see Horton and Ross 2003), which has the potential to affect worker productivity in jobs throughout the economy. Finally, the increased worker productivity due to greater caloric intake and improved nutritional status leads to economic growth, which is a necessary (although not sufficient) condition for increasing the living conditions and incomes of the poor.

The effects of lower retail prices for rice are reinforced by farm diversification in response to lower farm prices for rice. As rice prices decline, more farmers will be encouraged to produce other crops and livestock that are more nutritious. Not all farmers will shift crops because the production of other crops and agricultural products is often riskier than rice, but the increased production from some farmers will in turn serve to lower prices of these items, thus making them more affordable for the poor. The second important long-term indirect contribution of lower rice prices to poverty alleviation is that this helps to accelerate the structural transformation of the economy.

Long-term poverty alleviation requires the creation of jobs in the relatively higher-productivity industrial and service sectors of the economy. This is obviously true if one is trying to reach the urban poor. It is also true for the long-term reduction in rural poverty, because no country in history has managed to grow rich while keeping a large share of its population in agriculture. This is a striking empirical regularity of the development process (Timmer 1988). In other words, long-term poverty alleviation requires a structural transformation of the economy away from agriculture and toward industry and services.

Low rice prices that are the result of higher productivity induced by agricultural research contribute to this structural transformation of the economy. Low rice prices allow nominal wages to be lower without sacrificing any welfare on the part of the workers, because their effective purchasing power increases with lower rice prices. In conjunction with other factors (e.g., a stable macroeconomic environment, an efficient and fair legal system), these lower wages stimulate the job creation and growth that are necessary for sustainable poverty alleviation. If rice prices are high, workers will legitimately demand higher wages. But these higher wages will discourage investment, both domestic and foreign, and the growth process will be retarded.

But it is not possible to accelerate the growth process simply by pursuing policies that arbitrarily depress rice (food) prices through subsidies. This strategy has been tried, and it has not worked. If low retail prices are accompanied by low farm prices in the absence of rising productivity, farmers have little incentive to produce, leading to reduced supplies of food. In conjunction with high levels of consumption encouraged by low prices, this results in black markets and high prices for those without privileged access to cheap food. Alternatively, if low retail prices are accompanied by high farm prices through the use of subsidies in the absence of rising productivity, the typical result in developing countries is large government fiscal deficits that cannot be sustained or that reduce funds available for other critical investments such as education, health, and infrastructure. Thus, it is critical to have low prices that are the result of higher productivity, not low prices achieved through other means.

Negative effects of low prices

Of course, there can also be negative effects from the lower prices that are the inevitable result of increases in agricultural productivity in a market economy. It is true that lower rice prices, *holding all else constant*, adversely affect poor rice farmers who produce a surplus of rice. However, it is misleading to couch the issue in terms of lower prices with all else held constant, because the lower prices are the consequence of higher yields and increased multiple cropping that serve to increase supplies faster than demand. These higher yields and increases in harvested area lead to sharply increased production that compensates farmers for the lower prices. Lower prices do hurt farmers with a surplus to sell who have not adopted innovations or diversified their cropping systems into higher-value crops. Thus, it will be important to ensure that even poor farmers have the ability to adopt innovations such as C₄ rice. This should not be a problem if C₄ rice is developed in the public sector, which will likely make it available to all farmers without licensing fees. Even if C₄ rice were developed in the

private sector, such companies do not want to charge prices so high that no farmers can adopt the innovation. But private companies may still charge prices that are high enough that small farmers are indeed excluded. With this possibility in mind, it will be important to develop arrangements such as those that were developed for “golden rice,” for which the private sector has donated intellectual property so that poor farmers will be able to save their own seed (IRRI 2005).

As another example of a possible negative effect, lower rice prices can reduce the wages of poor farm laborers by reducing the demand for farm labor, although this effect will not always be present (FAO 2006b). Working against this adverse outcome are rising farm yields due to increased productivity, which will tend to increase the demand for farm labor and raise wages for landless laborers. The net effect of these two changes is ambiguous.

To summarize, the main point of this section is that agricultural research has complex effects that affect all poor people in the entire economy, not just rice farmers (who are a minority of the poor). Further, the vast majority of these effects are beneficial, as will be seen in the next section.

Agricultural research and poverty alleviation: evidence

The main papers that directly measure the effects of agricultural research on poverty reduction are by Shenggen Fan and colleagues at the International Food Policy Research Institute (IFPRI). For the case of India, Fan et al (2000a) show that government expenditures on agricultural research and development (R&D) have a larger impact on rural poverty in India than any other expenditures aside from roads. If urban poverty is included, then agricultural R&D have a larger impact on total poverty than any other government expenditure (Fan 2002). Fan et al (2000b) show that agricultural R&D also have a large impact on rural poverty reduction in China, second only to the effect of education.

These studies show not only that agricultural research contributes to poverty alleviation, but that the marginal effects on poverty of a dollar spent on research are larger than the effects of a dollar spent on other public goods such as irrigation, roads, electricity, or education (except in the case of China for the latter). This is not to say that these other investments are not important—they are. However, money spent on agricultural research appears to do more for poverty reduction than money spent on other investments.

Other studies show results that are generally consistent with these findings, although the analysis is not as direct. For example, Thirtle et al (2003), using cross-country data on poverty and yields, find that a 10% increase in yields is associated with a 4.8% decline in poverty in Asia. Datt and Ravallion (1998) show that a 10% increase in farm yields in India reduces rural poverty by 9%, with the effect on incomes being strongest for the poorest of the poor (i.e., those far below the poverty line). From these studies, it is just a short step to conclude that agricultural research (without which higher yields are difficult to achieve) is important for poverty reduction.

A large group of other studies examines the effects of economic growth on poverty alleviation, and in particular the effects of agricultural growth (as distinguished from nonagricultural growth). Nearly all studies agree that economic growth contributes to poverty alleviation, and many present evidence showing that agricultural growth in particular contributes more to poverty alleviation than nonagricultural growth, mainly because a given dose of agricultural growth has a larger effect on poverty than the same dose of nonagricultural growth (Timmer 1997, Ravallion and Chen 2004, Christiaensen et al 2006). In some respects, this is not surprising because of the greater importance of agriculture for the incomes of the poor and the greater importance of food in the expenditures of poor consumers. In addition, agricultural growth also seems to generate more nonagricultural growth through various backward and forward linkages than the other way around.

Not all studies agree with these conclusions on agricultural growth versus growth in other sectors. For example, Ravallion and Datt (1996, 2002) find that growth in the service sector does more to alleviate poverty than growth in agriculture. Bravo-Ortega and Lederman (2005) find that nonagricultural growth raises incomes for the poorest quintile more than does agricultural growth. Nevertheless, these studies do find that agricultural growth reduces poverty.

Key trends in the Asian rice economy

Rice prices

As late as 1981, world market rice prices were in excess of \$1,000 per ton (in inflation-adjusted 2005 US dollars), similar to the average that prevailed from 1950 to 1980. Since then, however, there have been two episodes of major price declines: 1981 to 1986, when prices declined by 66%; and 1998 to 2001, when prices declined by 48% (from the new lower base). Both of these declines were due (in part) to large increases in production (Dawe 2002). Since 1980, rice prices have declined more rapidly than maize and wheat prices. Although most Asian governments do not allow changes in world prices to be directly transmitted to domestic markets, domestic rice prices (after adjusting for inflation) are also lower in many Asian countries than those 40 years ago.

The new lower prices are due in large part to the lower per ton production costs made possible by the Green Revolution. These lower prices have allowed the poor improved access to calorie supplies, and the proportion of undernourished Asians has declined sharply.

By 2001, world prices reached a record low of \$190 per ton for Thai 100B, a high-quality indica grain commonly traded in world markets. Four years later, however (2005), world rice prices had increased to \$288 per ton, an increase of 51% from the record low in 2001. (Despite this increase, prices in 2005 were still below the average of \$391 per ton from 1986 to 1998.) An important question, then, is what will be the evolution of future rice prices? It is not possible to predict commodity prices with much precision, but some key trends that will affect future prices will now be discussed.

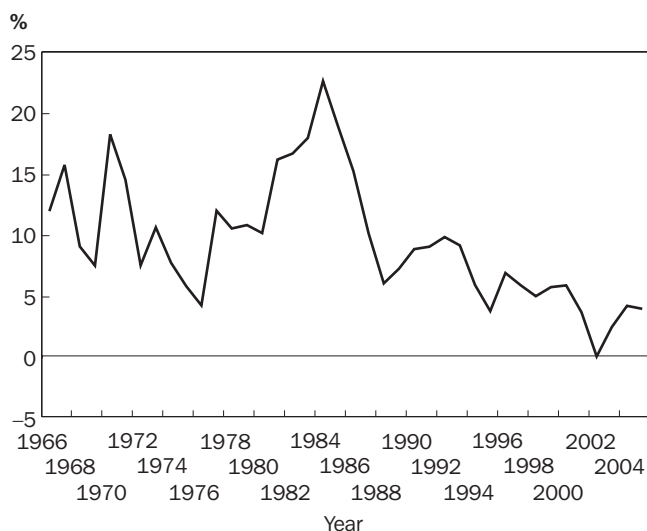


Fig. 1. Cumulative percent change in rice yield during the previous 5 years in rice-producing Asia. Source of raw data: FAO (2006a). Rice-producing Asia refers to Bangladesh, Bhutan, Brunei, Cambodia, China, Democratic People's Republic of Korea, India, Indonesia, Japan, Laos, Malaysia, Myanmar, Nepal, Pakistan, Philippines, Republic of Korea, Sri Lanka, Thailand, Timor-Leste, and Vietnam.

Trends in area, yield, and the adoption of modern varieties

Much of the 139% increase in rice production in Asia between 1965 and 1999 came from higher yields. Perhaps surprisingly, however, the area harvested to rice increased by 23% during this period despite the loss of some land to urbanization,² as irrigation and shorter-duration varieties allowed many farmers to grow multiple crops of rice per year. Since 1999, however, rice area harvested has been declining from its peak. This process has been most rapid in East Asia, where area harvested in 2004 was 10% below its peak five years earlier. However, even for the rest of Asia combined (South and Southeast Asia), rice area harvested in 2004 was 3% below the 1999 level (data for the calculations in this paragraph come from FAO 2006a). Thus, it seems unlikely that expanded area will be a major source of future growth in rice production (unless prices were to increase substantially and encourage farmers to shift into rice).

Rice yields continue to increase, but this rate of increase has slowed tremendously in recent years. While cumulative increases of 10% every five years were typical up until the early 1990s, yields in 2004 were just 3% higher than in 1999 (see Fig. 1). Some of the dramatic slowdown in yield growth (and the decline in area harvested) may be due to the low level of prices, as farmers find that growing other crops, or

²These losses are much smaller than is often supposed, however. See FAO (2006b) for some brief discussion.

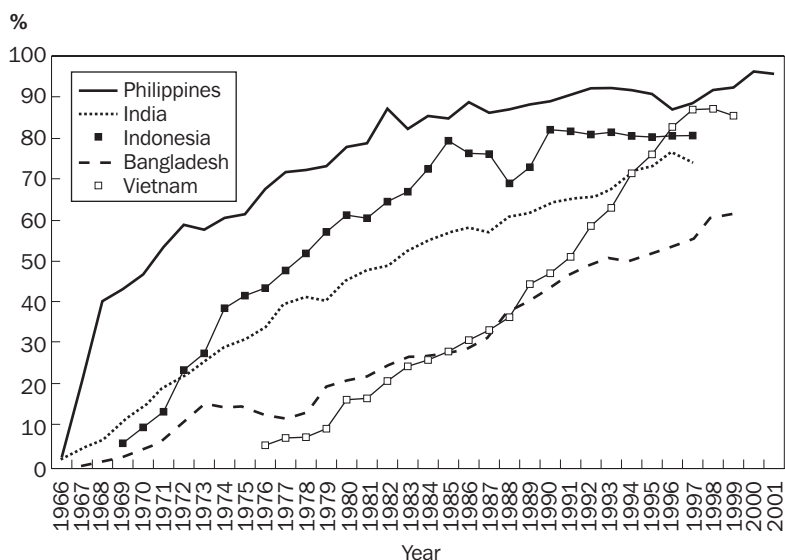


Fig. 2. Percent adoption of modern rice varieties, selected Asian countries, 1966 to 2001. Source of data: IRRI (2006a).

leaving agriculture altogether, is more profitable, and they devote less attention to management of their rice crops. On the other hand, growth in the adoption of modern varieties has slowed down as adoption rates reach plateaus of 75% to 90% in many countries (see Fig. 2; further adoption is probably constrained because not all rice-growing areas have adequate water supplies). Furthermore, rice yields have remained stagnant in recent years in Indonesia (an increase from 4.43 tons per hectare in 1997 to just 4.52 tons per hectare in 2004), despite large increases in domestic rice prices during that period due to government restrictions on imports. This suggests that higher prices may not bring forth higher yields in the current environment. Instead, it may be that yields are constrained by a lack of post-Green Revolution yield-enhancing technologies that are available and are being communicated effectively to farmers. If true, this situation is much more worrisome than if slow yield growth were due only to low prices for farmers.

Hybrid rice is one possible solution to this lack of new technologies, and adoption is increasing in several countries. Putting aside the case of China, where it has been widely adopted for decades, hybrid rice has made the most progress in recent years in northern Vietnam, the Philippines, and India (see Fig. 3). At this stage, it is not clear how much hybrid rice will be able to boost rice yields in the medium to longer term. Adoption has been quite rapid in the Philippines, but it may have been fueled to some extent by government subsidies. It is not clear whether farmers will return to inbred modern varieties once these subsidies are withdrawn.

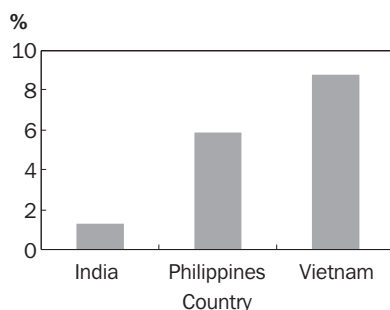


Fig. 3. Percent adoption of hybrid rice, selected Asian countries, 2004. Source of data: IRRI (2006b). Data for Philippines refer to 2005.

Future rice demand growth

While slowing yield growth may portend future price increases, population growth continues to slow in the region, which will help to reduce pressure on future rice prices. After growing by 2.4% per year in the early 1970s in rice-producing Asia, the population expanded by just 1.2% per year from 2000 to 2005. The most recent medium variant forecast from the United Nations projects that total population in these countries will grow just 29% between 2005 and 2050 (UN 2006), after which the population will soon begin to decline in absolute terms in the region.

Reinforcing the trend of slower population growth is the decline in per capita rice consumption that occurs as countries become wealthier. This decline is due to the universal human desire to diversify diets noted by Bennett's Law, which states that the proportion of calories in the diet coming from starchy staple foods (including cereals and roots and tubers) declines as incomes increase. In addition to diversifying away from cereals toward livestock, dairy products, fruits, and vegetables, Asian diets are also diversifying within the class of cereals. Since most Asians eat rice as their primary staple, this typically means shifting from rice toward wheat (rice remains dominant, but less so).³The net result can be seen in Japan, for example, where rice consumption has declined from 111 kg of milled rice per capita per year in 1961 to just 57 kg in 2003. Similar declines have taken place in the Republic of Korea (141 kg per capita per year in 1978 to 78 in 2003) and Malaysia (127 kg per capita per year in 1974 to 71 in 2003). As more Asian countries continue on the path of economic growth, per capita rice consumption will continue to decline.

³However, there are other cases where consumers who eat diets based on wheat (northern India, northern China) or maize (southern Philippines) are shifting from those staples toward rice.

Fertilizer prices, petroleum prices, and biofuels

World market prices in 2005 for urea, the most important source of nitrogen for rice in Asia, were nearly triple those in 1999 due to higher prices for petroleum and natural gas. Nevertheless, prices are still slightly below their level of ten years earlier after adjusting for inflation. And these prices are substantially below the levels reached during the late 1970s and early 1980s in the face of repeated shocks on world petroleum markets.

It is extremely difficult to forecast how petroleum and urea prices will evolve during the next 20 years. While there are legitimate concerns that higher prices are here to stay, the world economy has weathered previous disruptions to petroleum markets. For example, prices rose sharply from 1972 to 1981 due to a succession of problems in the Middle East, but then declined sharply to very low values. But this time may be different, because of increased demand from China and other rapidly developing economies that is likely to be more permanent.

Permanently higher urea prices are not likely to cause major disruptions on the world rice market, however, because urea represents only about 10% of the gross value of production. Thus, even if prices were to double again from their elevated current levels, an increase in rice prices of 10% would be enough to keep farm profitability constant and keep land in production.

A more worrisome possibility is that high petroleum prices will lead to substantially increased demand for biofuels from sugar and maize. If more ethanol plants are built and production continues to expand, demand for sugar and maize will increase, leading to higher prices of these crops if sufficient additional production is not forthcoming through either expansion of area or higher yields.⁴ Higher prices will substantially increase the profitability of growing these crops, and Asian farmers may be induced to substitute land out of rice, for example, shifting from a rice-rice rotation to rice-maize. The resulting decrease in rice supply would put upward pressure on rice prices.

The possibility for substantial disruptions in rice markets would seem to be nontrivial. A report from OECD (2006) estimates that ethanol from sugarcane in Brazil and from maize in the United States is a competitive source of transport fuel at oil prices of \$44 per barrel (\$29 in the case of Brazil), which was below the price of oil in most of 2005 and the first half of 2006. Further, at current levels of agricultural and ethanol production technology, the report estimates that, if oil prices are sustained at \$60 per barrel, prices for sugar in 2014 will increase by about 80% relative to a scenario of constant (at the levels prevailing in 2004) biofuel production, with maize prices increasing by 20% (no calculations were done for rice). This calculation ignores the possibility of bringing fallow land into production and using international trade, so it is only vaguely indicative of how world markets will evolve, and clearly more research is needed in this area. Nevertheless, these increases are substantial, especially since the increased biofuel production that would result will raise the share of biofuels in

⁴Demand will also grow for bio-diesel made from oilseed crops.

total EU-15 transport fuel consumption to just 6%, and less than 3% in the U.S. and Canada. Thus, there would appear to be substantial upside potential if biofuels were to become even more important as a source of transport fuel. Indeed, if biofuels were to account for 10% of total transport fuel, this would require nearly one-third of all land currently harvested for cereals, oilseeds, and sugar in the U.S. and Canada, and more than 70% in the EU-15 (OECD 2006).⁵ Recalling Senauer and Sur's (2001) estimate that a 20% increase in food prices would increase the number of undernourished in Asia by 158 million, the impact of biofuel demand is worrisome indeed.

Higher petroleum prices may also lead to higher production costs in terms of fuel for tractors and combine-harvesters. However, most rice production in Asia is not highly mechanized, with labor being the main component of production costs. Thus, higher fuel prices will not substantially affect rice production costs through this channel. But production costs of maize and wheat in developed economies could be substantially affected, and, to the extent that this drives up prices for wheat and maize on world markets, rice markets can be affected through crop substitution on the supply side as noted above.

Water scarcity

Water scarcity is also a potential constraint to future rice production. At a macro level, Rosegrant et al (2002) project that consumptive water use for domestic and industrial purposes in Asia will increase by 98% and 88%, respectively, between 1995 and 2025. During the same period, consumptive use for irrigation will increase just 1%. But this approximately constant amount of irrigation water will have to support 50% higher levels of cereal production. In addition, because it is cost-prohibitive to move water long distances (the south-to-north water conveyance projects in China will be an exception), the role of markets and prices in allocating water to its highest-value use will be limited. In other words, while it may be possible to shift water to higher-valued uses within a basin, it will not be possible, for example, for the Philippines to sell surplus water to northern India.

Although many areas will continue to have adequate supplies of water for decades to come, there will be shortages localized in space and/or time. For example, in the Zhang He irrigation system in Hubei, China, competition from domestic and industrial uses has substantially reduced the volume of water available for irrigation during the past 40 years (Hong et al 2001; see Fig. 4). Although there were increases in water productivity during this time, rice production started to decline during the 1990s (although other factors such as labor scarcity may have also contributed to this outcome).

Periodic widespread water shortages may also become more common in the future if global warming leads to more variable weather patterns. One example is the El Niño Southern Oscillation (ENSO) phenomenon that has been shown to affect rice

⁵This calculation assumes current agricultural yields and current levels of transport fuel consumption. Both are likely to increase, so it is not clear if the reported calculation is biased up or down.

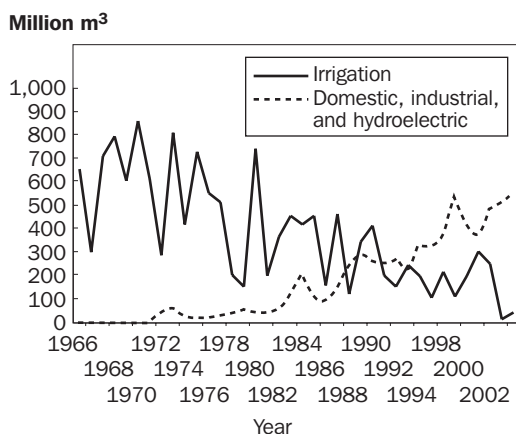


Fig. 4. Water allocations by sector, Zhanghe Reservoir, Hubei, China, 1966 to 2003. Source of data: Hong et al (2001) updated with unpublished data from Zhanghe Irrigation District.

production in India, Indonesia, the Philippines, and Sri Lanka (Selvaraju 2003, Naylor et al 2001, Falcon et al 2004, Zubair 2002). For example, rice production in the dry season declined by 27% in the Philippines during the El Niño of 1997-98. Since dry-season production accounts for nearly half of annual production, this drought required substantial additional quantities of imports.

Given increased future water scarcity, the implications for rice prices are potentially severe if water management is not improved. Under the “Crisis” scenario of Rosegrant et al (2002), rice prices in 2025 are higher by 80% than in a “Business as usual” scenario.

Diversification of farm household income

In addition to scarcity of natural resources, farmers will also experience a scarcity of time for farm management in the future. Farms throughout Asia are diversifying into nonfarm activities such as trading, construction, services, and transportation, among many others. Pingali (2006) states that, on average, 32% of farm household income in Asia comes from nonfarm activities. Furthermore, this share is increasing over time. Hossain et al (2000) found that the share of rural household income coming from nonagriculture in four selected Philippine villages increased from 36% to 60% between 1985 and 1997. Nearly all—96%—of the households surveyed in 1997 had income from agriculture, so these rural households are not abandoning farming entirely.

As farmers find less time to devote to farm management, it will become critical to develop technologies that do not require large investments of knowledge or time on the part of farmers; otherwise, farmers may not adopt the technologies. C_4 rice could be particularly useful in this regard, because the knowledge is embodied in the seed. Farmers may need to make some adjustments in cultivation techniques with C_4 rice, but these are likely to be minor.

The difficulty of part-time farmers applying knowledge-intensive technologies in Asia is compounded by the fact that farm sizes are very small, typically 1 to 2 hectares compared with farm sizes of more than 100 hectares in countries such as the United States and Australia. Farmers with small amounts of land under their control have less incentive to learn sophisticated crop management methods, because the benefits of higher yields on a small plot of land are not likely to compensate for the fixed cost of knowledge acquisition. The benefits of increased yield on large plots of land have a much greater chance of covering the fixed costs.

Land consolidation could remedy this problem, and farm sizes will eventually increase as development proceeds in Asia. But this process of consolidation could turn out to be quite slow. For example, the average farm size in Japan increased from 1.00 ha in 1960 to 1.57 ha in 2002. In Korea, average farm size rose from 0.88 ha in 1970 to 1.46 ha in 2002 (Fan and Chan-Kang 2003). These increases are not very large, less than a hectare in 30 to 40 years.

Conclusions

The main objective of the paper has been to show that agricultural research aimed at raising productivity has an important role to play in poverty alleviation. If C_4 rice is technically feasible, it would make a very important contribution in that regard. Higher yields would increase rice supplies, helping to lower rice prices for the poor and allowing farmers to diversify into other important crops without sacrifices in aggregate rice production at the country level. Higher yields would also contribute to higher farm profits, although the net effect would be ambiguous because of lower prices in the long run.

C_4 rice that increased grain yield per unit of water transpired would make an important contribution to managing future water scarcity in Asia, which would contribute to both poverty alleviation and environmental goals. C_4 rice would also increase nitrogen-use efficiency, reducing production costs per ton for farmers and helping to reduce nitrogen loads in the environment.

Furthermore, although some trends in the rice economy give cause for optimism regarding the future path of rice prices, other trends raise concerns that prices will increase in the next 20 years. Clearly, a great deal of uncertainty surrounds any projections that are made. The possible effects of climate change have also not been considered, adding a further layer of uncertainty.

In such circumstances, it seems prudent to provide solid funding for additional research on C_4 rice. If the optimistic scenario holds (e.g., oil prices return to low levels, demand for biofuels does not increase substantially, population growth declines rapidly, diets diversify away from rice quickly, water management improves), the added productivity from C_4 rice will still contribute to making poverty alleviation even more rapid than it otherwise would have been. In other words, the faster that cereal prices decline, the faster that undernourishment will become a distant memory. But, if a more pessimistic scenario unfolds, many poor people will suffer severely from

the resultant high prices. C₄ rice would provide an important buffer to make sure this eventuality does not come to pass.

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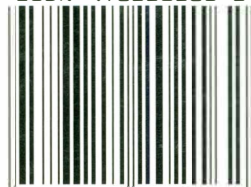
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Notes

Author's address: Senior food systems economist, Food and Agriculture Organization Regional Office for Asia and the Pacific, Bangkok, Thailand.

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