

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

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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"

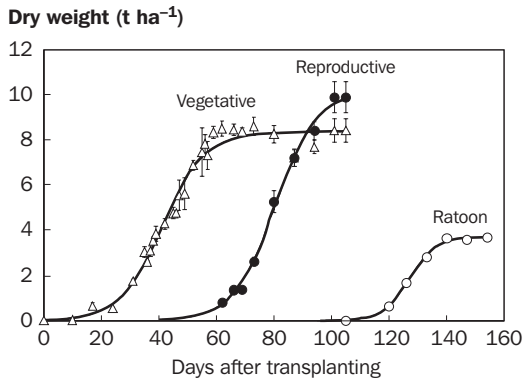


Fig. 1. The triphasic crop growth pattern for irrigated rice in the dry season at IRRI, Los Baños, Philippines. Each phase is represented by a sigmoid curve of the form $y = a/(1 + \exp[-(x - b)/c])$, where y is dry weight, x is time (days after transplanting, DAT), a is the asymptote ($t\ ha^{-1}$), 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 $t\ ha^{-1}\ ^\circ C^{-1}$ (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 (phyllonchroon) 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

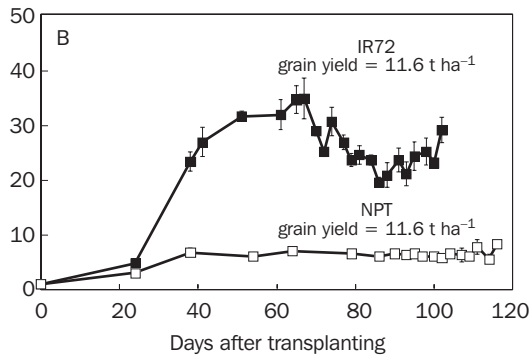
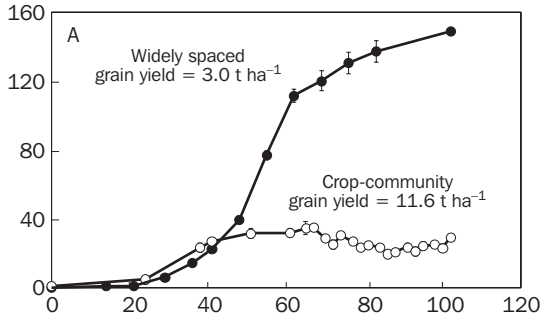
$$l_i = L_{\max}/N \quad (2)$$

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 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

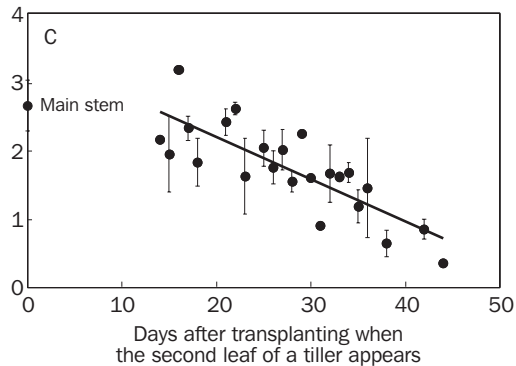


Fig. 2. (A) Tiller number of widely spaced and crop-community plants of irrigated rice IR72 in 1997 dry season; **(B)** tiller number of crop-community plants of irrigated rice IR72 and NPT in 1997 dry season; IR72 has the same data as in (A) plotted at higher resolution. Grain yields at 14% moisture 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); $y = -0.062x + 3.43$, $r^2 = 0.65$. In addition, the weight of the panicle of the main stem is shown.

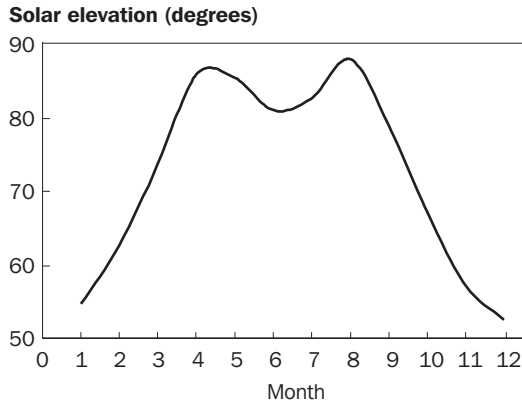


Fig. 3. The annual pattern of maximum solar elevation (mid-month) at IRRRI, Los Baños, Philippines (14°11'N). Source: NOAA Solar Position Calculator at www.srrb.noaa.gov/highlights/sunrise/azel.html.

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-

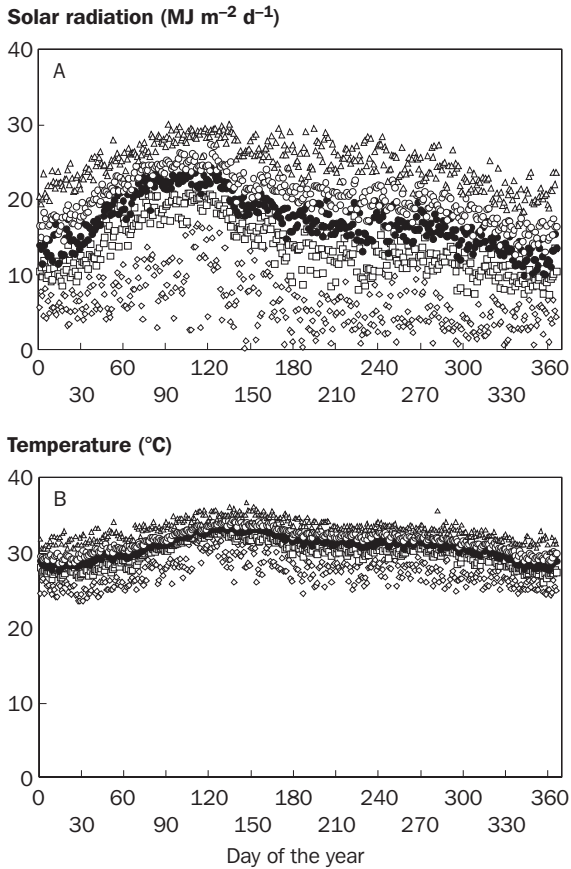


Fig. 4. Annual patterns of (A) solar radiation and (B) maximum temperature at IRRI, Los Baños, Philippines; data extracted from the IRRI weather database (1979-2005); daily median, ●; third quartile, ○; first quartile, □; absolute maximum, ▲; absolute minimum, ◇.

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

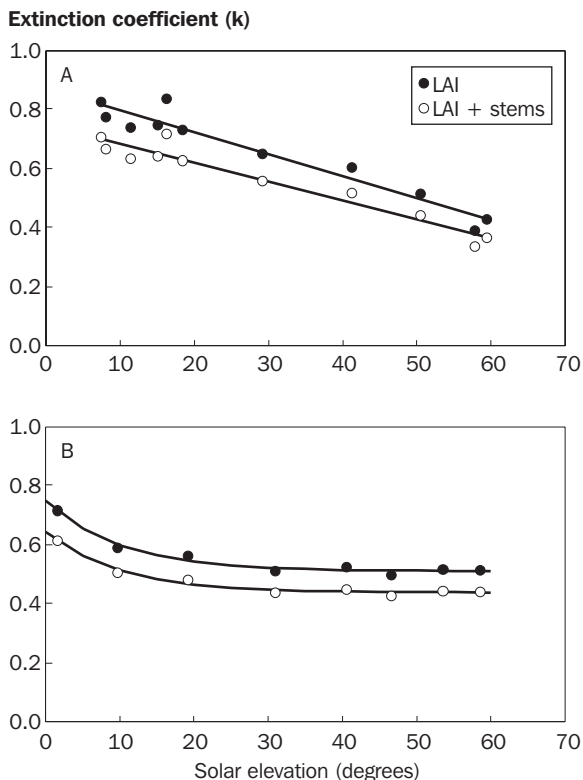


Fig. 5. Values for the extinction coefficient at different solar elevations calculated for LAI and LAI + stem area index (shoot) under (A) direct (LAI: $y = -0.0075x + 0.87$, $r^2 = 0.93$; LAI + stems: $y = -0.0064x + 0.75$, $r^2 = 0.93$) and (B) diffuse light conditions (LAI: $y = 0.51 + 0.24 \exp(-x/9.94)$,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

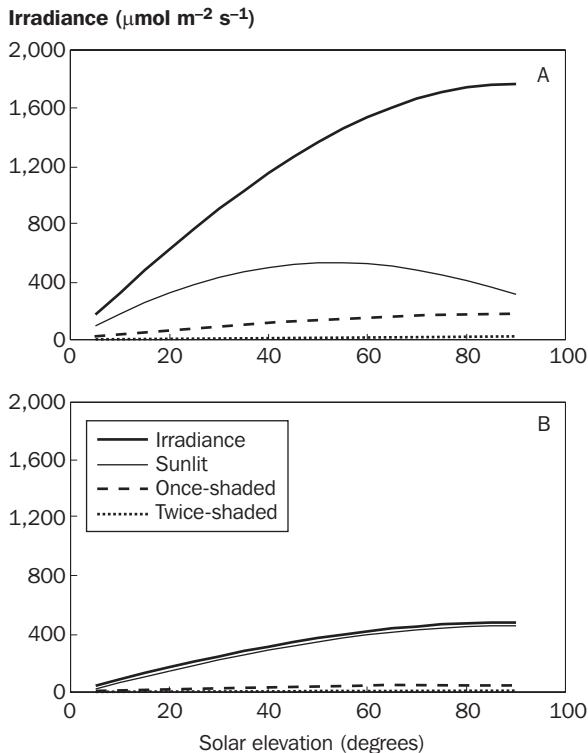


Fig. 6. The irradiances of sunlit, once-shaded, and twice-shaded leaves of an IR72 rice canopy under (A) direct and (B) diffuse light conditions for irradiance conditions in mid-April at Los Baños, Philippines ($14^{\circ}11'N$, $121^{\circ}15'E$, altitude 21 m). Note that incident PAR is for a horizontal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

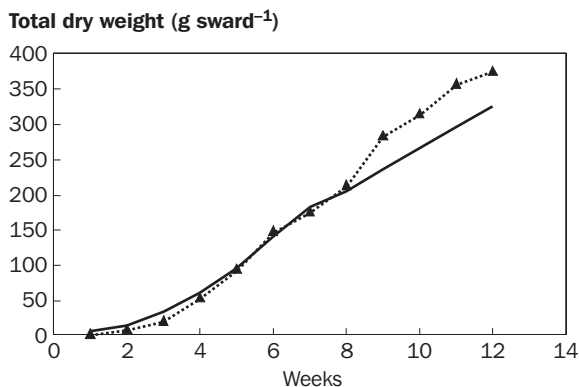


Fig. 7. The relationship between cumulative biomass production (\blacktriangle) and cumulative measured canopy gross photosynthesis (—, hexose equivalent dry weight) in swards of perennial ryegrass (after Robson 1973).

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 greenhouse. 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 ($33 \text{ }^\circ\text{C}$) than

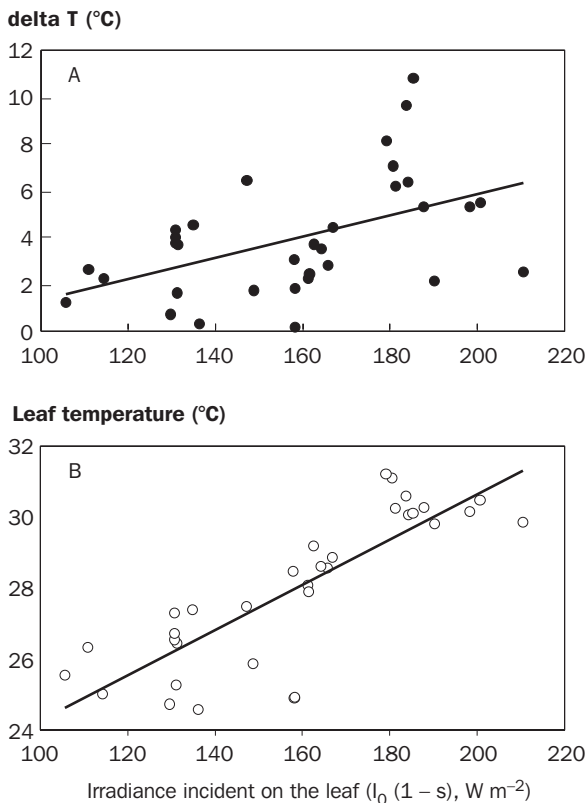


Fig. 8. (A) The relationship between the difference between leaf and air temperature and irradiance incident on the leaf for nontranspiring leaves of rice ($y = 0.045x - 3.17$, $r^2 = 0.24$). (B) The relationship between leaf temperature and irradiance incident on the transpiring leaf in rice ($y = 0.064x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

the C_3 leaves ($31\text{ }^\circ\text{C}$), but both were less than air temperature ($34.5\text{ }^\circ\text{C}$). The results suggest that leaf temperatures in rice could increase by about $2\text{ }^\circ\text{C}$ 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_l) 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 Buttimore 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.

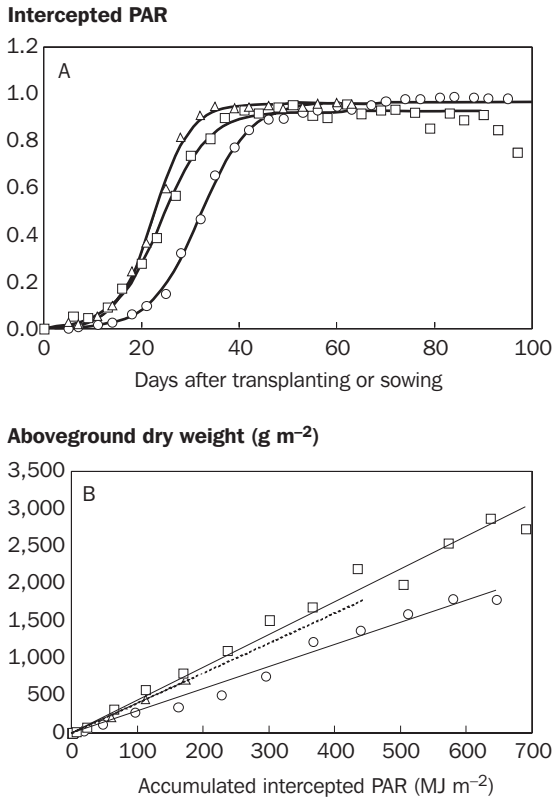


Fig. 9. (A) The time courses of fractional intercepted PAR during crop growth following transplanting (rice (IR72), ○; *Echinochloa glabrescens*, △) or sowing (maize, □). The fitted curves are of the form $y = a/(1 + \exp(-(x - b)/c))$ and are used simply to highlight the differences; note that interception 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 *Oryzae*, 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 μmol mol⁻¹ and PEP carboxylase activity of about 3 μmol min⁻¹ 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.

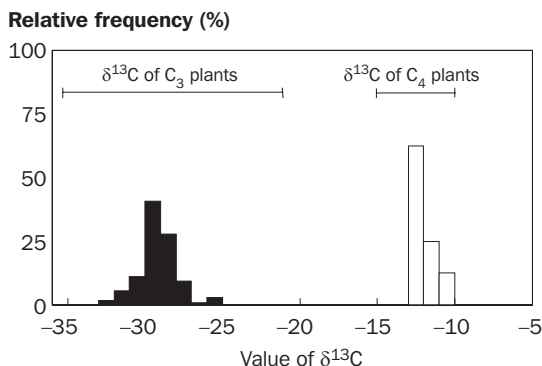


Fig. 10. Distribution of $\delta^{13}\text{C}$ values of the representative subsample of wild rice (■) and a small collection of C_4 plants (□). The range of $\delta^{13}\text{C}$ values for C_3 and C_4 plants shown is from Cerling (1999).

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

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Acknowledgment: We gratefully acknowledge the scientific and financial support given for this work by Dr. Robert S. Zeigler, without whose enthusiasm the C₄ conference would not have taken place.