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Commentary

Photosynthate allocations in rice plants: Food production or atmospheric methane?

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Atmospheric methane is recognized as one of the most important greenhouse gases. Sources of atmospheric methane are about 1/3 natural and 2/3 human-caused (1). Its concentration has roughly doubled in the past 100 years. This increase and any future continuation of it can affect Earth's climate through global radiative forcing (increased forcing to date is between 0.5 and 0.7 $W \cdot m^{-2}$) (2). Thus, methane is the second most important anthropogenic greenhouse gas after CO_2, whose radiative forcing to Year 2000 is 1.4 $W \cdot m^{-2}$.

Flooded rice fields are a significant source of atmospheric methane. Worldwide emission from rice has been extrapolated from reports from China, India, Vietnam, Korea, and the Philippines to be from 21 to 30 teragrams per year (1 teragram = 10^{12} g) (3). These values are less than several estimates since 1981, but still represent a globally significant source.

Rice is the staple food for nearly 50% of the world's peoples, many in Asia. The world per capita rice consumption in 1990 was 58 $kg \cdot yr^{-1}$ of milled rice. This represents 23% of the average world per capita caloric intake and 16% of the protein intake (4). Because rice is such an important food source for much of the world, it is imperative to develop ways of reducing the impact of rice agriculture on the global atmosphere and subsequent climate change. An important finding that may lead to such a reduction while also increasing rice production is presented in the article appearing in this issue of PNAS by Denier van der Gon *et al.* (5). These researchers demonstrated that an inverse relationship exists between a rice plant's capacity to store photosynthetically fixed carbon as grain and seasonally emitted methane. Under a common set of climatic and agricultural conditions, lower methane emissions are observed from plots that contain rice plants with higher numbers of filled grain spikelets, indicating that plants that more closely approach their potential yield limit emit less methane to the atmosphere. These data support the hypothesis that higher methane emissions observed in the tropical wet season as opposed to the dry season (6) are associated with lower harvest index values resulting in excess carbon that could not be allocated to rice grain. This excess carbon is then available to soil bacteria for the production and emission of additional methane.

An inverse relationship exists between a rice plant's capacity to store photosynthetically fixed carbon and seasonally emitted methane.

To meet the increased rice demand of a growing global population, rice cultivation must continue to expand at or beyond its current rate. If current population trends continue, by 2020, ≈1.2 billion new humans will be added to Asia alone. It is projected that the world's annual rough rice production must increase from the 1990 value of 473 million tons to 781 million tons by 2020, and over a billion tons by the next century. Because arable land is limited in major rice growing areas because of increased urbanization, increased production has to be achieved mainly by intensifying cropping (i.e., two or three crops per year) and developing new higher yielding rice cultivars rather than expanding the area of rice cultivation. Irrigated rice will continue to dominate production. Irrigated rice land now comprises about half of the total harvested area, but contributes more than two-thirds of the total grain production (7).

As we move into the future, rice grain production must increase to feed an increasing population, while at the same time, methane emissions from irrigated rice agriculture need to be reduced to help stabilize the global climate. Thus, the relationship between rice grain yield and the emission of methane from irrigated rice fields emerges as a major scientific and policy issue.

Methane emission from rice fields is the result of a complex array of soil processes involving plant microbe interactions. Flooding rice fields promotes anaerobic fermentation of carbon sources supplied by the rice plants and other incorporated organic substrates. Methane emission is the net result of opposing bacterial processes—production in anaerobic microenvironments, and consumption and oxidation in aerobic microenvironments, both of which can be found side by side in flooded rice soil. This process is diagrammed in Fig. 1.

Major substrates for the methanogenic bacteria are derived from root exudates, lysates, and dead organic material derived from senescent rice plants and incorporated vegetation (8, 9). Several specific low molecular weight organic substrates are produced in the process of mineralization that are in turn converted to methane by methanogenic bacteria (10, 11). Thus, variations in the rate of production (and emission) of methane, which is the terminal product of this plant-microbe system, ultimately depend on variations in parameters that determine the physiological state of the rice plant, such as nutrient supply, temperature, sunlight, and water.

Under ideal cropping conditions, where climate factors and the availability of carbon substrates from sources other than rice plants are similar, the level of observed methane emission is positively correlated with the rice plant above ground and below ground biomass (8). This observation can be interpreted to mean that photosynthetically produced carbon is allocated within the rice plant in a fairly uniform fashion. The ratio of carbon allocated to above ground biomass to that allocated to root processes and subsequent methane production remains essentially constant over time.

Different levels of photosynthetic activity can be experienced in temperate and subtropical regions by varying the rice planting date (9). If the source of organic substrate

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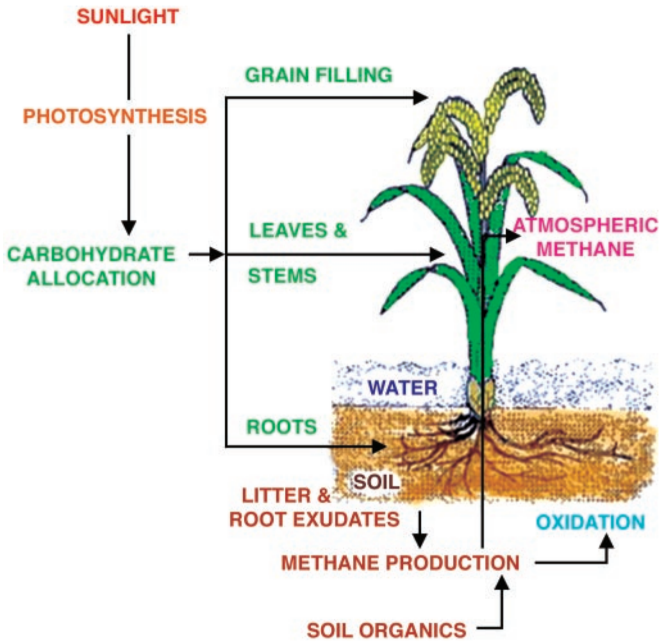

Fig. 1. Diagram representing the climate-plant-soil components of the processes of rice grain production and methane emission.

for methanogenesis is from the rice plant, then the effect of planting date on methane emission should correlate with effects on the rice plant. Critical factors caused by differences in planting date that affect the growth and development of rice plants in a region such as the Texas Gulf Coast are soil temperature, soil moisture content, and solar radiation (12). In temperate zones, the optimal temperature for rice plant development varies for different growth stages (13)—normally between 20°C and 31°C during the vegetative stage (12) and between 21°C and 35°C during the reproductive and maturity stages (14).

Lack of sunlight early in the growth and development of the rice plant normally does not limit grain yield except under excessively cloudy and cool conditions. However, panicle differentiation begins a 42-day critical sunlight-requiring period (15). Low yields do occur in years of low sunlight caused by cloudy conditions and rain. These conditions also produce taller plants and severe lodging (12). These same seasonal effects of low yield with increased plant height and biomass have been duplicated in shading experiments and in experiments in which solar radiation was changed by employing different planting dates during the same year (12). Date-of-seeding tests indicated that yield is directly correlated with cumulative sunlight units during the critical light-requiring period. Approximately 60% of the yield variability observed in these tests was caused by sunlight levels at the critical period. For every 1% reduction in total sunlight, a 2.2% reduction in yield was observed over a 5-year period (12). Yoshida and Parao (16) found a similar correlation between grain yield and sunlight during the reproductive stage in Japan—for every 1% reduction in accumulative sunlight, a 0.73% reduction in yield was observed. These authors also show a smaller effect of sunlight changes on grain yield during the vegetative and ripening stages. Yoshida (13) used these data and estimates of photosynthetic efficiency to develop a relationship between solar radiation and potential maximum grain yields.

The photosynthetic activity of rice plants also correlates with methane production and emission (9). If one hypothesizes that the allocation of photosynthates to various parts of the rice plant system increases with photosynthetic activity, the amount of biomass productivity and produced methane should both be proportional to the amount of solar radiation the plant receives. This was found to be true. A 1% reduction in the solar radiation received during the critical growth period (heading ± 21 days) resulted in a 1.11% ($r^2 = 0.99$) reduction in grain yield and a 1.70% ($r^2 = 0.75$) reduction in methane emission. Although the effect of reduced radiation on methane emission is somewhat larger than that on grain yield, these results strongly suggest that rice grain filling and methanogenesis are similarly related to photosynthesis and that plant activity is tightly coupled to both methane production and emission.

The positive correlation of methane emission with biomass is very well documented (8, 17, 18). The negative correlation between methane emission and grain yield observed during five successive years of tropical wet and dry seasons in the Philippines (6) is interpreted by Denier van der gon *et al.* (5) as not necessarily being in conflict. Rather it illustrates the complex nature of the system. Considering the Philippine data (Table 1 in ref. 5), note that there is not only no correlation shown between aboveground biomass and seasonal methane emission, but there is no correlation between grain yield and aboveground biomass. In fact the harvest index is far from constant over the several wet or dry seasons. Three different cultivars are represented in this data set, but even for a single cultivar there is no uniformity in the harvest index. Evidently, other variables are influencing the system and grain yield is not a true predictor of methane emission. Denier van der gon *et al.* (5) realized this and conducted a set of experiments in which they reproduced the effect by excising varying fractions of the developing spiklets on the rice plants. This treatment caused a lowering of the grain yield and a partial reallocation of the potential grain carbon to methane formation. These authors then observe that unfavorable conditions for spikelet formation in the wet season may similarly explain high methane emission and that this effect provides opportunities to mitigate methane emissions by optimizing rice productivity.

These conclusions are timely and a call to action. Rice, as C3 plants, are not in general as efficient in their utilization of solar energy as other grain crops such as corn. The potential yields of some rice cultivars are as high as 10 ton per hectare (ha), but actual yields are generally between 3.30 and 8.36 ton per ha. Plant breeders, primarily at the International Rice Research Institute in the Philippines have now raised the potential yield of a new rice-plant type to 12 ton per ha, which may well be close to the theoretical limit for rice. With such new cultivars designed for specific climates and pest resistance along with outstanding agricultural practice, farmers may be able to approach 75% or 80% of the theoretical (potential) yield limit. If that goal could be reached, the increased rice grain production needed to feed the world of 2100 might become a reality. If in so doing, the additional allocation of photosynthate carbon to grain and away from the production of methane might help reduce the effects of global heating enough to prevent a reversal in the losses in grain yield through increased heat-induced spikelet sterility. The food demands of an increasing world population and the disruptive effect of global warming both challenge the agricultural science community to pay attention to how these two environmental pressures interact and to accelerate efforts to develop higher yielding, farmer-friendly rice that emits less methane.

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