

Learning about positive plant-microbial interactions from the System of Rice Intensification (SRI)

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Summary

Biological scientists are increasingly addressing the interactions of genetic potential and environmental influences (G×E interaction) to understand the mechanisms for resulting phenotypic expression of such potential. This body of epigenetic knowledge has focused on the level of molecular biology but needs now to deal more with interactions at the level of organisms, e.g. plants and microbes that affect each other's development and performance. The System of Rice Intensification (SRI) which originated in Madagascar in the 1980s shows how by altering age-old management practices for plants, soil, water and nutrients, rice genotypes can produce dramatically more productive plant phenotypes. These yield more grain with less input of seeds, water, fertilizer and even labour. The practices in particular produce much larger and longer-lived root systems, and these are associated with increased and modified populations of soil biota. This paper summarizes what is known about these dynamics from field studies and experimental data.

Key words: Biotic and abiotic crop stresses, crop yields, endophytes, epigenetics, rice production, soil microbiology, symbionts, System of Rice Intensification, water saving

Introduction

Justus von Liebig's understanding of soil-plant nutrient relationships, summarized in his 'Law of the Minimum', left an indelible mark on the discipline of soil chemistry for a century and a half in part because of his vivid imagery that portrayed soil nutrient supplies as 'barrel staves' of different lengths (van der Ploeg *et al.*, 1999). Few know, however, that by the end of his long and productive career, Liebig had come to distrust his soil-chemistry preoccupation for explaining soil-plant nutrient interactions. By the end of his career, Liebig expressed a greater appreciation of the biological factors that drive soil dynamics (Liebig, 1995; Uphoff *et al.*, 2006).

Perhaps even more influential as a metaphor that has shaped scientific thinking in the realm of biology has been Charles Darwin's drawing of 'the tree of life' in his seminal book *On the Origin of Species* (1859). This diagram delineated the different kingdoms of life, most notably the flora and fauna, as branching off from an upward-growing collection of creatures that biologists were engaged in classifying systematically to make sense of the plethora of organisms that inhabit the earth, seen and unseen.

The concept of a ‘tree of life’ implied a hierarchy that placed animals (and particularly *Homo sapiens*) above the other creatures as the most advanced because they were the most recently descended. This is now strongly challenged by phylogenetic reconstructions of this ‘tree’ (Puigbò *et al.*, 2009). But there are other reasons for moving away from this ‘tree’ conception, even if molecular analysis can now provide a more fine-grained dendritic appearance to tree-of-life diagrams. The limitations of Darwin’s imagery are not remedied by accounting for the complexities of horizontal gene transfer.

Tree-like concepts for representing the evolutionary relationships among nature’s organisms can be a guide for classifications and can summarize our understanding of life on earth. But unfortunately they project a retrograde understanding of life’s origins and its perpetuation, representing defensible taxonomy but biased biology. The kingdoms of flora and fauna never really ‘branched off’ from the bacterial and fungal kingdoms, by implication ‘leaving them behind.’ Instead, we should be always mindful that all plants and animals have persistent, pervasive relationships with the much smaller, simpler organisms that are essential to the survival of all (Margulis & Sagan, 1997; Margulis, 1998).

The System of Rice Intensification

The System of Rice Intensification (SRI) – an alternative methodology for rice (*Oryza sativa*) cultivation (Laulanié, 1993) developed in the 1980s in Madagascar – offers some instructive insights into this conference’s focus on ‘positive plant-microbial interactions’. SRI makes changes in age-old practices for managing rice plants, soil systems, irrigation and soil nutrient amendments that can increase crop yields by 50–100%, and sometimes by more, while at the same time reducing farmers’ requirements for seed, water, fertilizer, agrochemicals, and often even labor (Stoop *et al.*, 2002; Uphoff, 2003; Uphoff & Kassam, 2009).

How SRI could enable farmers to produce more from less was initially difficult to understand, appearing ‘too good to be true.’ There was considerable skepticism, even opposition, expressed in the peer-reviewed literature (Dobermann, 2004; Sheehy *et al.*, 2004; Sinclair & Cassman, 2004; McDonald *et al.*, 2006). However, evidence continues to accumulate that the ideas and suite of practices which constitute SRI, when used together, can evoke more productive phenotypes from practically all rice genotypes, such as shown in Fig. 1.

SRI methods have proved beneficial for use with ‘unimproved’ local varieties as well as with higher-yielding varieties and hybrids. Higher productivity with alternative methods has been seen in a wide range of countries, such as China (Yuan, 2001; Zhao *et al.*, 2009), Gambia (Ceesay *et al.*, 2006), India (Satyanarayana *et al.*, 2006; Sinha & Talati, 2007), Indonesia (Sato & Uphoff, 2007), Myanmar (Kabir & Uphoff, 2007), and Sri Lanka (Namara *et al.*, 2008).

Acceptance of SRI was slowed in part by the fact that it is so different from Asia’s ‘Green Revolution’ based on: (a) breeding new ‘improved’ varieties that are more responsive to external inputs (and then getting farmers to buy and use these) and (b) persuading farmers to increase use of external inputs -- more mineral fertilizer, more water, and agrochemical crop protection. SRI methods, on the contrary, do not require either the use of new varieties or external inputs. Farmers can raise their yields by continuing to plant whatever varieties they are already using, generally with less seed, water, fertilizer, agrochemicals, and even in many cases with less labor (Uphoff, 2007). These positive effects are, however, quite counter-intuitive.

Explaining Unanticipated Increases in Factor Productivity

Producing ‘more with less’ is anomalous since our culture as well as science have led to the expectation that we must always increase our expenditures and investments if we want to raise production and income. This is, however, a perspective based on engineering or economics, which proceeds from a different paradigm than that of biology. While biology, like engineering and



Fig. 1. These two rice plants grown on the farm of Sr Luis Romero in San Antonio de los Baños, Cuba, are both the same age (52 days after germination) and same genotype (VN 2084 variety). Both started in the same nursery, but when 9 days old, the plant on the right now with 42 tillers was transplanted into a field managed according to SRI methods: wide spacing, aerobic soil conditions, more organic fertilization. The plant on the left with five tillers was kept in the nursery, relatively crowded, for transplanting at the usual stage in Cuban practice (50–55 days). The following season, a video was made to document sequentially the differentiating growth of rice plants on Romero's farm (<http://ciifad.cornell.edu/sri/countries/cuba/SICAenglish.wmv>). Photo by Dr Rena Perez.

economics deals with inputs and outputs, it is based on open systems with large amounts of free or potentially-free inputs. Thus, it operates according to somewhat different logic and principles, made tangible by SRI experience.

Some of the benefits deriving from SRI's alternative practices can be explained in terms of standard kinds of agronomic variables and performance. We will review them before proceeding to consider plant-microbial interactions. Agronomic explanations depend (apparently) mostly on chemical and physical factors. These can account for many of the phenotypical gains achieved with SRI management in terms that are simpler and more easily validated than the more complicated processes of biology.

Effects of Crowding on Roots and Photosynthesis

SRI methods achieve higher yield with fewer plants, dramatically reducing plant populations by up to 80–90%. Traditionally, rice fields have been planted with clumps of 3–6 plants in a hill, and hills are 10–20 cm apart, in rows or at random. With SRI, on the other hand, single seedlings are transplanted in a square pattern, and usually with at least 25 cm spacing between plants. With 10–25 plants per m² instead of 50–100 or more, plant roots can spread in all directions,

and all leaves receive enough sunlight to be photosynthetically active. The close planting that is standard practice leads to constrained tillering and to shading of plants' lower leaves which makes them senesce early, especially from the latter phase of vegetative growth and thereafter. These leaves become, in effect, parasitic, consuming from the plant's supply of photosynthate rather than contributing to it.

Moreover, crowding of plants reduces the energy that is supplied to their roots for their metabolism since lower leaves are the main source of root systems' supply of photosynthate (Yoshida, 1981). There is a positive correlation between the chlorophyll content of the lower leaves and rice root activity and between the chlorophyll level in flag leaves and duration of grain filling (Mishra & Salokhe, 2008a). There are good reasons to explain how fewer plants can give more crop yield provided more attention is paid to their capacity for photosynthesis and tillering and to shoot-root relationships (Thakur *et al.*, 2009).

Effects of Flooding on Roots and Photosynthesis

For millennia, it has been assumed that rice plants benefit from inundation. Indeed, a leading text on rice production has stated this as established fact (DeDatta, 1981). Yet it is demonstrably true that rice roots growing under hypoxic conditions lose function and degenerate – by as much as 75% by the time of flowering (anthesis) when grain formation begins (Kar *et al.*, 1974). Under flooded conditions, about 30–40% of rice roots' cortex degrades to form air pockets (aerenchyma) that permit oxygen to diffuse passively within the roots (Kirk & Bouldin, 1991). This is an adaptation, however, not an ideal situation, as adequate supply of oxygen cannot reach root tips from which growth proceeds.

The root systems of plants growing in well-drained soils are larger and also lighter-coloured compared to those of continuously flooded plants, whose dark color indicates necrosis (Fig. 2). Greater root length density and greater number of lateral roots are found under non-flooded soil conditions compared to continuously flooded soil conditions (Mishra & Salokhe, 2008b). While it is true that rice plants can survive under conditions of inundation, they do not thrive that way.

The main benefit to farmers from flooding their rice fields is actually to suppress weeds, thereby saving labor otherwise required for weeding. Applying just enough water to meet the needs of the growing plant – and of the aerobic soil organisms that coexist with it in the rhizosphere (the soil layer surrounding plant roots) – is demonstrably better for plant health than flooding. It is thus explainable why reducing applications of irrigation water can enhance crop growth and productivity.

Effects of Transplanting Younger Seedlings

Transplanting older seedlings (3–4 weeks old or even older) requires less care than handling younger ones. Also, older plants are more resistant to certain biotic or abiotic stresses. But they have less potential for growth than do younger ones. If quite young seedlings (<15 days) can be established in the field, transplanted carefully and shallow, their resulting growth of both roots and tillers is demonstrably greater. This effect can be explained by an understanding of phyllochrons (Laulanie, 1993) because the 15th day is usually about when the 4th phyllochron of growth begins (Nemoto *et al.*, 1995). The best time for transplanting seedlings is during the 2nd and 3rd phyllochrons, when there is no tillering and no new roots after the main shoot emerges from the seed during the 1st phyllochron, i.e. usually between 5 and 15 days after sowing.

The productivity benefits from transplanting seedlings after the 1st but before the 4th phyllochron can be seen in empirical trials, although the effect is most evident when combined with the other SRI management practices (Mishra & Salokhe, 2008b). For years it was assumed that farmers



Fig. 2. Rice plant roots grown under mostly aerobic soil conditions of SRI management (left) and conventional flooded conditions (right). Photo by Bahman Amiri Larijani, Haraz Technical Development and Extension Centre, Amol, Iran.

cannot or will not transplant very young seedlings and thus this effect was not examined. We have found that once farmers see the benefits of this practice, most are willing to try transplanting small seedlings, even as young as 4–5 days old, with good effect. Learning SRI methods of transplanting requires additional time and effort at first; but once the techniques have been learned, transplanting many fewer and much smaller seedlings becomes easier and actually preferable for farmers (http://www.youtube.com/watch?v=TP4CV0L4_n4). (Note: SRI methods, which were devised for transplanted crop establishment, have been adapted in several countries for direct seeding. So this will open some new lines for investigation).

Effects of Greater Root Growth and Longevity

With root systems that are larger and not degenerating, rice plants can take up both more macro- and micro-nutrients. The differences in root systems seen from Figs 1 and 2 have been documented with systematic measurement of root length density (RLD) at different depths of soil and root-pulling resistance (RPR). The latter measure is the amount of force (in kg) required to uproot one or more plants. RPR is a summary measure of the friction that the total root system, including root hairs, has with surrounding soil and reflects the total surface area of the root system.

Barison (2003) found that SRI plants had considerably greater RLD in the lower soil horizons compared with roots of plants of the same variety conventionally grown in the same soil: 2.3 times more at 30–40 cm depth, and 3.8 times more at 40–50 cm. They also had greater RPR as SRI plants at the panicle initiation stage required 7.2 times more force per plant than rice grown with farmer methods. At maturity, this disparity had increased to 14.2 times. Such large differences in root growth are the most evident phenotypical differences induced by SRI practices. Because roots are the major interface between plants and beneficial microbes, they offer the most opportunities for consideration of positive interactions.

Grain yield correlates significantly with differences in root systems. Barison (2003) analyzed the production of 109 farmers in four regions of Madagascar who were using both SRI and conventional methods to grow rice. Crops on fields near to each other were evaluated so that the influence from differences in farms, farmers, soil and climate would be minimal. Average yields with SRI methods were 6.36 t ha⁻¹ compared with 3.36 t ha⁻¹ with standard techniques. Fig. 3 shows how the two sets of rice plants exhibited different capabilities for converting N uptake into grain. The same relationship was seen for P and K.

Understanding how this greater efficiency in producing grain for a given amount of macronutrients is achieved by SRI rice phenotypes will require further study. One hypothesis would be that plants having larger, deeper and longer-lived root systems are taking up not only more macronutrients but also greater amounts of micronutrients, which are essential for their synthesis of the enzymes that guide and sustain plant metabolism. More micronutrient uptake could enable plants to convert macronutrients more efficiently into the cells and tissues that constitute grain. On the other hand, with root systems remaining healthier and functioning longer and with plant leaves senescing later, so that photosynthesis is greater and continues for more time, the higher production may be linked to this more than to micronutrient uptake. Both sets of causation could, of course, be at work.

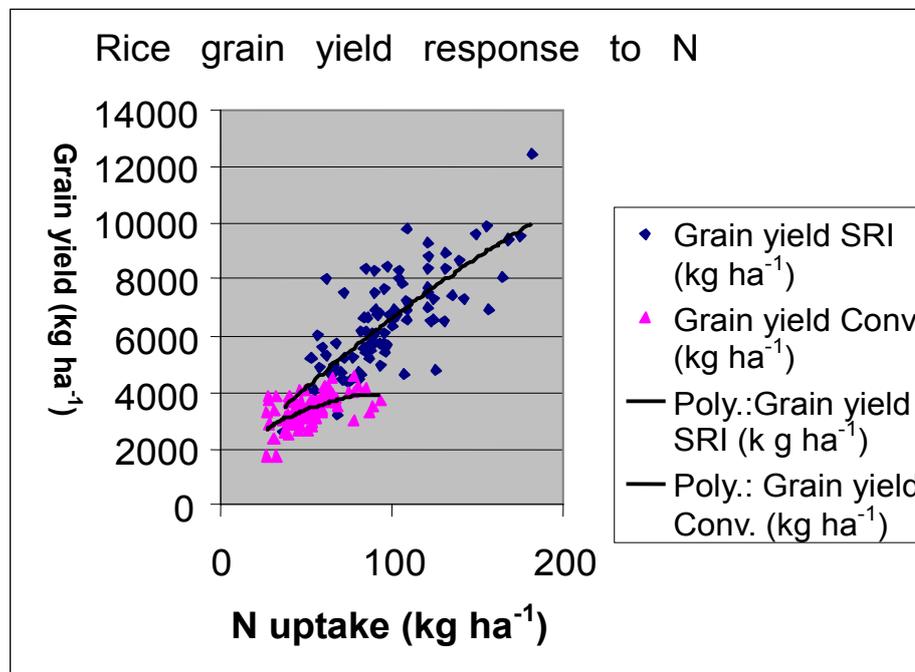


Fig. 3. Grain yield response as a function of nitrogen uptake for two sets of rice plants grown with SRI or conventional methods (N=109), four locations in Madagascar. Source: Barison (2003).

Another contributing factor to such plant performance could be greater microbial activity associated with larger root systems which is continuously involved in solubilization of non-available forms of nutrients. These are more plentiful in most soils than their available form. In a recent ICRISAT study, discussed below, unavailable sulfur was found to be 12 times more abundant, and boron 45 times more abundant, than amounts of available S and B (Rupela, 2009). Many microbes can convert unavailable forms of nutrients into available forms to meet the plant demands.

Looking Beyond Agronomics to Microbiology and Epigenetics

These explanations for superior performance of SRI rice plants are based on agronomic considerations that are reasonably straightforward and fairly easily evaluated, although this does

not mean that they are. As SRI experience accumulates, through our own investigations and becoming better acquainted with contemporary research findings, it becomes more apparent that there are soil biological elements operative in the root zones and in the rice plants themselves which are probably contributing to the results that we see with SRI management of plants, soil, water and nutrients, enhancing the abundance, diversity and activity of soil organisms.

These considerations were reviewed in Randriamiharisoa *et al.* (2006), based on what we knew or thought at the time of writing. Here we will try to go further, addressing issues or opportunities that relate to ‘positive plant-microbial interactions.’ In particular, SRI experience is raising questions that may probably be best addressed under the rubric of epigenetics, factors that regulate, accelerate or inhibit the expression of genetic potentials since we are seeing markedly different, and more productive, phenotypes repeatedly emerging from the same genotypes.

The differences in rice roots seen in Fig. 2 can be accounted for by agronomic factors, e.g., the effects of hypoxic soil conditions. The effects seen in Fig. 1, on the other hand, probably require explanations involving plant-microbial symbiosis. For example, the production of phytohormones by soil organisms could stimulate root growth that will benefit both the plant and associated microbes in the rhizosphere. This paper cannot and does not offer any firm conclusions on these questions because so much research remains to be done before satisfactory explanations can be put forward. However, it is hoped that the anomalies and possible ways of accounting for them discussed here will encourage others to join in investigations on SRI.

Initial Evidence and Inferences

The SRI methodology combining a fortuitous set of plant, soil, water and nutrient management practices was inductively developed for the challenging soil conditions with which Madagascar farmers have to work (Uphoff, 2006). The first large-scale validation of the methods developed by Laulanié was in the peripheral zone around Ranomafana National Park, whose soils had been evaluated for North Carolina State University and USAID by Johnson (1994, 2002). These soils were, in chemical terms, quite ‘poor’: very acidic, with pH levels ranging between 3.8 and 5.0, and affected by Fe and Al toxicity, and with cation exchange capacity (CEC) low to very low in all horizons. The parameter that appeared to be the most constraining was phosphorus (P) availability, however. Available P was measured as only 3–4 ppm, which is less than half the 10 ppm minimum expected to give acceptable crop yield. This was one reason why paddy yields in the area were averaging only 2 t ha⁻¹.

Yet somehow the smallholding farmers who took up SRI practices around Ranomafana during the three seasons 1994/95 to 1996/97 were able on these same soils to average 8 t ha⁻¹. They did not add any mineral P to the soils, just organic matter, mostly compost made from decomposed rice straw and other vegetative biomass (seldom any farmyard manure because most farmers were too poor to have cattle). How could such high yields be attained from these ‘deficient’ soils? Nitrogen could be enhanced through biological N fixation, utilizing atmospheric N which is abundant. But P is an essential macronutrient that operates more as a stock than a flow. However, a focus on available P overshadows the fact that in most soils, unavailable P is much more than the available P in the soil solution.

Phosphorus Solubilization by Bacterial Activity

A clue to how P deficits could be remedied by altering management practices came from a short research report published in *Nature* by Turner & Haygarth (2001). These authors had studied levels of available P in the soil solution at 29 locations in England and Wales. They found that when the soils were wetted and then dried, the levels of P in the soil solution increased by large amounts, between 185–1900%. For these researchers, interested in reducing the level of P in

environmental water supplies, this was not a welcome finding. But to agriculturalists working with both phosphorus and cash constraints, this was something positive.

Turner & Haygarth (2001) suggested that this flush of available P could be the result of population dynamics for species of phosphorus-solubilizing bacteria (PSB) and possibly fungi, which would increase during periods when the soil was aerobic, acquiring P from the ‘unavailable’ stock of phosphorus in the soil. This is P that is present inside convoluted soil particles that make phosphate ions inaccessible, or bound up in complex phosphate molecules that are mostly insoluble (Turner *et al.*, 2006). The stock of unavailable P is usually much greater, even orders of magnitude more, than the supply of available P in soils at any particular time (Russell, 1988). O Rupela, in evaluations of soils in India, has found usually *c.* 20 times more unavailable P than available P (unpublished).

When soil is flooded and becomes anaerobic, a fraction of the microbial cells in the soil will lyse and release their contents into the soil solution, creating a flush of nutrients. A similar effect for releasing nitrogen from soil microbes when soil flooding occurs has long been known (Birch, 1958.) When the soil dries again, the surviving PSBs (there are always some in aerobic to micro-aerophilic pockets in soil) begin their multiplication and acquisition of ‘unavailable P’ again. Subsequent research confirmed this mechanism for mobilizing phosphorus (Turner *et al.*, 2003).

Without intending any effect on soil nutrient status, SRI recommended keeping the soil mostly aerobic, moist but unflooded, adding small amounts of water daily, stopping applications for 3–6 days several times during the vegetative growth phase to let the topsoil dry out; or a water management regime of alternately flooding and drying the soil. Such a regime would mobilize otherwise unavailable P through PSB activity, an effect that would be greater if there is abundant organic matter in the soil to support the growth of microbes (Ayaga *et al.*, 2006).

Turner & Haygarth (2001) speculated that such microbial activity could be having a positive effect on the availability of other soil elements such as micronutrients. However, there is very little research of this sort on micronutrients. When micronutrients are evaluated, significant differences can be measured that are likely to be associated with microbial activity (Table 1).

Table 1. Total boron (B), sulfur (S), iron (Fe), zinc (Zn), and available B, S, Fe and Zn, in the soil samples collected from Suchde Farm, village Bajwada (MP) on 19.09.07 (units are mg kg⁻¹ soil, or ppm)

Treatment	Total B	Available B	Total S	Available S	Total Fe	Available Fe	Total Zn	Available Zn (DTPA-Zn)
Original soil	29.7	0.27	93	7.17	40442	15.6	133	0.83
Between heap	26.0	0.29	103	7.00	33550	11.7	108	1.08
Planted heap	27.0	0.32	94	7.60	34625	9.1	77	0.97
Below heap	26.7	2.29	420	18.93	33300	21.0	97	6.10
Mean	27.3	0.79	178	10.18	35479	14.4	104	2.25
SE±	1.11 ^{NS}	0.215 ^{***}	21.0 ^{***}	1.054 ^{***}	1641.1 ^{NS(0.06)}	2.48*	21.7 ^{NS}	0.293 ^{***}
CV%	7	47	21	18	8	30	36	23

* = Statistically significant at 0.05, *** = Statistically significant at 0.001, NS = Not statistically significant, NS (0.06) = Not statistically significant at *P* = 0.05, but values are statistically significantly different at *P* = 0.06. Source: Rupela (2009).

These data come from an evaluation done at the invitation of Mr. Deepak Suchde (Email: deepaksuchde@gmail.com) to evaluate his methodology for growing crops on small heaps, about 30 cm diameter and 30 cm high, mulched with grass and composed of specially prepared, compost-like soil, which he refers to as ‘Living Soil’ (Amrit Matti). The heaps are regularly watered with a highly diluted (10×) fermentation called Amrit Pani, with 1 kg fresh cow-dung, 1 L cow urine, and 50 g unrefined sugar (jaggary) added to 10 L water and fermented for 3 days. This mix when evaluated at ICRISAT was found to be very rich in agriculturally-beneficial microorganisms (Archival Report GT-CI, 2005–2006, pp 366–367).

Soil samples from the unplanted fallow area on the same farm (labeled as ‘original soil’ in Table 1) were used as a reference value for comparisons. Rego *et al.* (2007) report 0.58 mg, 8–10 mg, and 0.75 mg per kg soil, respectively, as critical limits for B, S and Zn. Processes of nutrient mobilization are well-documented in the literature (Turner *et al.*, 2006), but they are difficult to measure, occurring in open systems both aboveground and belowground (Wardle, 2002).

Soil systems have been supporting plant growth on the earth’s surface for over 400 million years without exhaustion of its soil nutrients. It is unlikely that with just the recycling of nutrients, even to the maximum extent feasible, these would have been sufficient to maintain soil fertility over such a long period, without some continuous enhancement of soil nutrient supplies through chemical, physical, and (especially?) biological processes that mobilize sub-surface reserves through microbial activity and the actions of plant roots, especially perennials.

Endophytic Effects of Bacteria in Rice Roots

The first data we obtained on changes in microbial activity associated with SRI practices came from Andriankaja (2001), who examined, among other things, the populations of the N-fixing bacteria *Azospirillum* in the roots of rice plants grown under different management regimes. This was part of a multi-factorial evaluation with six factors and random block design, having 240 plots, 2.5 × 2.5 m². Data in Table 2 are averages for six replications, obtained from four treatments on the same clay soil: standard farmer practice without any soil amendments; SRI practice without soil amendments; SRI practice with NPK amendments; and SRI practice with compost additions.

Table 2. *Endophytic Azospirillum* populations associated with rice yield and tillering with alternative cultivation practices and nutrient amendments, on clay soil, Beforona, Madagascar

	Yield (t ha ⁻¹)	Tillers (plant ⁻¹)	<i>Azospirillum</i> count in roots (10 ³ mg ⁻¹)
Conventional cultivation without nutrient amendments	1.8	17	65
SRI cultivation methods without nutrient amendments	6.1	45	1,100
SRI cultivation methods with NPK amendments	9.0	68	450
SRI cultivation methods with compost amendments	10.5	78	1,400

Source: Data are from Andriankaja (2001) as reported in Randriamiharisoa (2002). Data are from replicated trials (N=6) of the respective treatments with RBD on 2.5 × 2.5 m plots.

Measured grain yields were, not surprisingly, closely related to the number of grain-bearing tillers per plant. But the almost six-fold production increase associated with SRI practices combined with compost amendments, compared to farmer practice without any amendments, was quite remarkable. It could have been dismissed as implausible if there had not been similar increases seen on some farmers’ fields in Madagascar.

The most interesting results were the numbers of *Azospirillum* counted in samples of root mass taken from the respective plots and analyzed at Institut Pasteur in Antananarivo.

- The yield achieved with *farmer practices and no soil amendments* – 1.8 t ha⁻¹ – was on a par with the national average rice yield in Madagascar. The associated *Azospirillum* population was 65,000 mg⁻¹ of sampled root biomass.
- When SRI practices were used with no soil amendments, the number of *Azospirillum* shot up to 1.1 million mg⁻¹; this increase was associated with a tripling of grain yield, to 6.2 t ha⁻¹.
- When *NPK fertilizer* was added with SRI practices, yield went up by 50% more – to 9.1 t ha⁻¹. However, the population mg⁻¹ of *Azospirillum* in the roots declined by 60%, an effect often seen when large amounts of inorganic nutrients are added to the soil. The increased yield was supported by enhanced supply of inorganic N.
- When *compost* was used with SRI methods instead of NPK, there was a further yield increase of 17% with SRI methods, to 10.2 t ha⁻¹. Given that the *Azospirillum* population went up to 1.4 million mg⁻¹, this increase was attributable to the availability of N through biological processes.

It should not be concluded that these changes are due just to variations in the population of *Azospirillum*, however. This species was chosen for analysis because it was relatively easier and more reliable to count than other microbes. So, *Azospirillum* should be regarded here as a proxy or indicator for overall levels of endophytic bacteria in the plant roots.

What contributions were made to higher yield, and how, by *Azospirillum* and the other soil organisms which were enhanced by SRI practice with compost supplementation was not studied and cannot be indicated here. Certainly more N must have been taken up and utilized by the rice plants for them to achieve the higher yields. But the yield enhancement may not have been simply or even primarily through N fixation by *Azospirillum*, even though this is a capability of these bacteria.

Dazzo & Yanni (2006) in their study of endophytic rhizobia in rice plant roots found a significant and positive effect on yield and grain protein content from soil bacteria residing in roots. However, they did not find any evidence of N fixation. Unfortunately for our understanding of plant-microbial interactions, these are enmeshed in exceedingly complex processes in nature, so we need to rely more on evidence than on plausibility, and we need an understanding of this complexity to be able to fit the various elements together.

Effects of Active Soil Aeration

Data from farmers using SRI practices around Ranomafana National Park in Madagascar pointed to a positive effect on yield from aerobic soil organisms. When paddy fields are not kept continuously flooded, there will be more weed growth, which necessitates control measures. The SRI strategy for weed control is to use a simple mechanical hand weeder pushed up and down, and across, the rows between plants. This implement churns up the top 3–5 cm of soil and buries weeds. When these weeds decompose, this provides additional nutrients to the soil and plants (Thiyagarajan *et al.*, 2005). But possibly of more importance is the provision of nutrients by beneficial aerobic microorganisms in the soil: such weeding may stimulate the growth of these microorganisms. SRI recommends that such weeding be done at 10–12 day intervals after transplanting, until plant canopies become too dense to permit more weeding.

Many SRI farmers do only the minimum of 1 or 2 weedings, enough to keep weeds in check; but others do 3 or 4, or possibly more. This practice adds active soil aeration to the passive soil aeration that results from SRI water management practices which, as seen above, can enhance the growth of phosphobacteria and possibly of N-fixing bacteria by alternatively wetting and drying the soil.

In the 1997–98 cropping season, the data shown in Table 3 were collected on the practices and results for 76 farmers in the Ambatovaky area west of the Park, gathered by a reliable field worker. These were not controlled experiments, so not all of the other practices were necessarily the same. But the results reflected realistic field conditions, and the differences seen are great enough that they should interest soil scientists and microbiologists to investigate these relationships further. Rice production in the area averaged 2–3 t ha⁻¹ at the time. SRI practices without active soil aeration could double yields, while doing the minimum of 1–2 weedings, enough to control weeds if well done, gave tripled yield. While doing a 3rd or 4th weeding was not needed for weed control, it increased yields by another 2–4 t ha⁻¹ with little added cost.

Several years later, a similar effect was seen in data gathered from 412 farmers in the terai (plains) of Nepal. Most farmers (N=366) did the recommended two weedings, which gave them a

Table 3. *Effects of active soil aeration using soil-aerating mechanical weeder in Madagascar and Nepal*

Mechanical weedings	(N)	Area/Harvest (ha kg ⁻¹)	Yield (t ha ⁻¹)
Madagascar: 1997–98 main season, Ambatovaky area (N=76)			
None	2	0.11 / 657	5.97
One	8	0.62 / 3,741	7.72
Two	27	3.54/26,102	7.37
Three	24	5.21/47,516	9.12
Four	15	5.92/69,693	11.77
Nepal: 2006 monsoon season, Morang district (N=412)			
	(N)	Range	Yield (t ha ⁻¹)
One	32	3.6 - 7.6	5.16
Two	366	3.5 - 11.0	5.87
Three	14	5.85-10.4	7.87

Sources: Madagascar: Data collected by Association Tefy Saina field staff, Ranomafana; Nepal: Data collected by District Agricultural Development Office, Biratnagar.

yield 700 kg ha⁻¹ more than doing just a single weeding, and almost twice as much as the average yield that these farmers got from conventional methods, 3.1 t ha⁻¹. The 14 farmers ambitious enough to do a third soil-aerating weeding were repaid for their efforts with 2 t ha⁻¹ more yield on average (Table 3). The average yields and upward shifts in these two countries are different because soil biological conditions and dynamics are location-specific but that there is a yield response to mechanical weeding is evident.

There were no systematic differences in the levels or kinds of soil fertilization that the farmers applied to their fields, so a tenable inference is that stimulation of greater populations of aerobic soil organisms such as phosphobacteria – whose growth would also have been enhanced by alternating the wetting and drying of soil – was contributing to the observed differences in yield associated with frequency of soil-aerating weeding. Other methods of weed control, by hand or with herbicides, contribute less to yield (Randriamiharisoa, 2002; Pandey, 2009).

Passive soil aeration, resulting from not keeping fields continuously flooded and letting them dry out, even to the surface-cracking point, several times during plants' vegetative growth, is surely necessary for active soil aeration to be effective. When soil is mostly aerobic, mycorrhizal fungi can thrive and provide rice crops with the benefits that most other terrestrial plants receive from these symbionts' services.

Perhaps because it has been assumed for so long that rice is best grown under inundated conditions, little research has been done on the effects of mycorrhizal fungi on rice production. There is some evidence that rice yields are adversely affected by their absence (Ellis, 1998; Ilag *et al.*, 1987).

Further, it is reported that even in unfavorable flooded soil environments, mycorrhizal inoculation of irrigated rice plants can increase their yield by 10% (Solaiman & Hirata, 1997). Presumably even more benefit can be obtained from enhancing mycorrhizal fungi in rice roots under more aerobic soil conditions.

Effects and Analysis of Microbial Populations in the Rhizosphere

The anomalous results of SRI rice production methods have become more comprehensible as experimental evaluations have been done, particularly in China (Wang *et al.*, 2002; Tao *et al.*, 2002; Zhu *et al.*, 2002), and as diverse contributions to the scientific literature have helped to account for different aspects of SRI phenomena. Although much remains to be evaluated and learned, what we know now reinforces this conference's concern with positive plant-microbial interactions. That more profuse root growth and delayed root senescence result from SRI management practices can be easily seen. These create a larger and healthier domain of longer duration for plant-microbial interactions to occur belowground, with many times greater root surface area. What cannot be so readily observed in the rhizosphere is expansion and change in microbial populations, including microbial root endophytes that colonize and inhabit plant roots.

It is well known that certain plants benefit from the nitrogen 'fixed' by rhizobial bacteria that inhabit nodules on the roots of leguminous species. However, biological N fixation (BNF) occurs also in the root zones of gramineae (grass family) species, which have no root nodules (Döbereiner, 1987). Among the gramineae, the most widely cultivated crop species which benefits from BNF is rice (Boddey *et al.*, 1995). A great variety of microbes that live around, on and in the roots of gramineae species can fix atmospheric nitrogen into forms available for plant use, producing nitrogenase enzymes to facilitate this. Other microbes, the phosphorus-solubilizing bacteria discussed above, produce the enzyme phosphatase that enables them to mineralize phosphorus into available forms which plants can utilize.

These and various other microbes also produce phytohormones such as auxins and cytokinins that stimulate plant growth, and particularly root growth such as seen in Fig. 1 (Frankenberger & Arshad, 1995; Khalid *et al.*, 2006). These plant growth-promoting and -regulating substances are extremely difficult to study because each of the hormones appears to have a number of different roles and functions in plant development. Further, they have effects at critical but usually over very short time periods during plants' development cycles. Truly miniscule amounts are often responsible for results that are manifested later and elsewhere in the plant, making uncontroversial research findings hard to achieve.

One of the effects of plant-microbial interactions is induced systemic resistance (ISR) which protects against certain pathogens (Kloepper, 1994; van Loon *et al.*, 1998; Heil & Bostock, 2002). We have not been able to explore how SRI practices might affect these various mechanisms for plant growth promotion and ISR but several evaluations, reported below, have found that SRI practices have a positive impact upon the frequency of certain beneficial microorganisms. Such shifts could be contributing to the more robust, productive phenotypes of rice that are induced by SRI management.

Researchers at Tamil Nadu Agricultural University in India began examining the effects of SRI management on rhizosphere bacteria in 2001. Gyathry (2002) found that introducing changes in seedling age, intercultivation with a mechanical weeder, unflooded irrigation and including green manure with fertilizers had a positive effect on the populations and activities of beneficial organisms in the soil rhizosphere.

At the active tillering stage, the numbers of all bacteria were 58% higher in SRI rhizospheres than for those of the same variety of rice plants grown conventionally, in the same bulk soil; *Azospirillum* populations were 53% greater; *Azotobacter* 127% greater, total diazotrophs (N-fixing bacteria) 60% more, and phosphobacteria 77% higher (Table 4).

Table 4. *Microbial populations in the rhizosphere soil in rice crop under different crop management conditions, Coimbatore, India, wet season, 2001–02*

Parameter	Treatment	Crop growth stage ¹			
		Active tillering	Panicle initiation	Flowering	Maturity
Total bacteria	Conventional	9.35	14.91	9.73	7.64
	SRI	14.66	21.64	10.99	7.51
<i>Azospirillum</i>	Conventional	4.69	7.39	3.13	1.42
	SRI	7.17	9.08	4.23	1.52
<i>Azotobacter</i>	Conventional	8.88	25.57	10.45	5.56
	SRI	20.15	31.17	10.92	6.45
Total diazotrophs	Conventional	9.11	10.52	7.14	4.71
	SRI	14.62	22.91	7.68	5.43
Phosphobacteria	Conventional	9.15	17.65	7.76	2.28
	SRI	16.19	23.75	13.79	2.66

¹Numbers are square root transformed values of population per gram of dry soil.

Conventional: 24-day-old seedlings; irrigating to 5 cm depth one day after disappearance of ponded water; hand weeding twice; recommended fertilizers; SRI: 14-day-old seedlings; 2 cm irrigation, after hairline cracks in the soil surface appeared, up to panicle initiation (PI); after PI, irrigate one day after disappearance of ponded water; inter-cultivation with rotary weeder four times at 10-day intervals; recommended fertilizer plus green leaf manure. Source: Gyathry (2002).

Table 5. *Microbial activities in the rhizosphere soil in rice crop under different crop management conditions, Coimbatore, India, dry season, 2002*

Parameter	Treatment	Crop growth stage				
		Active tillering	Panicle initiation	Flowering	Grain filling	Maturity
Dehydrogenase activity ($\mu\text{g TPF g}^{-1}$ soil 24 h ⁻¹)	Conventional	81	263	78	24	16
	SRI	369	467	139	95	42
Urease activity ($\mu\text{g NH}_4\text{-N g}^{-1}$ soil 24 h ⁻¹)	Conventional	189	1794	457	134	87
	SRI	230	2840	618	228	173
Acid phosphate activity ($\mu\text{g p-Nitrophenol g}^{-1}$ soil h ⁻¹)	Conventional	1800	2123	957	384	214
	SRI	1984	2762	2653	995	686
Alkaline phosphate activity ($\mu\text{g p-Nitrophenol g}^{-1}$ soil h ⁻¹)	Conventional	261	372	332	124	120
	SRI	234	397	324	189	146
Nitrogenase activity (nano mol C ₂ H ₄ g ⁻¹ soil 24 h ⁻¹)	Conventional	-	3.15	7.63	-	1.94
	SRI	-	3.70	11.13	-	1.87

¹Square root transformed values of population per gram of dry soil.

Conventional: 24-day-old seedlings; irrigating to 5 cm depth one day after disappearance of ponded water; hand weeding twice; recommended fertilizers; SRI: direct sowing of sprouted seeds; 2 cm irrigation after hairline crack up to maturity; inter-cultivation with rotary weeder four times at 10 day intervals; recommended fertilizer plus green leaf manure. Source: Gyathry (2002).

In Gyathry's study, microbial activity in the rhizosphere soil, as reflected in measures of enzyme levels, representing processes of N and P mobilization and uptake, were also significantly greater at almost all phases of crop growth (Table 5). While the reasons for these differentials are not clear, such differences have been found in other research.

An evaluation of the productivity of SRI methods supported by the Worldwide Fund for Nature (WWF) in Andhra Pradesh state of India starting in 2004 included systematic field studies of soil biota led by a microbiologist at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT). The soils of paddy fields managed according to SRI recommendations and comparable fields – on the same farms and managed by the same farmers – where conventional practices were used were compared in terms of chemical, physical and biological properties.

Out of some 200 farmers participating in the evaluation funded by WWF, the soil characteristics of 27 farms in four districts whose farmers were willing to cooperate in the study over four seasons were analyzed in depth. Average yields over this period were 7.68 t ha⁻¹ with SRI cultivation methods vs 6.15 t ha⁻¹ with farmers' usual practices (Rupela *et al.*, 2006).

Significant differences in the growth of SRI root systems, as discussed above, were confirmed in this study (Table 6). Indeed, the differences were quite dramatic. Rice plants in the SRI plots had about 10 times more root mass, about five times more root length density, and about seven times more root volume in the top 30 cm of soil profile, compared with roots in the plots of flooded rice. Root length in the top 15 cm of soil on these fields was 19.8 km m³ vs 2.4 km m³ (Rupela *et al.*, 2006).

Table 6. *Root dry weight (g m⁻³), root length density (m m⁻³), and root volume (cm³ m⁻³ soil) of rice in top 30 cm soil profile at harvesting stage from ten farmer's fields, Andhra Pradesh, India, rainy season, 2006*

Depth	Root oven dry weight (g m ⁻³)			Root length density (m m ⁻³)			Root volume (cm ³ m ⁻³ soil)		
	SRI	Conv.	Mean	SRI	Conv.	Mean	SRI	Conv.	Mean
0–15 cm	392	19	206	19820	2386	11103	3391	252	1822
15–30 cm	193	19	106	10572	2243	6408	1740	242	991
SE+		34.7*	27.5***		1816.2*	1501.0***		292.5*	234.5***
		(38.9)			(2122.7)			(331.6)	
Mean	293	19		15196	2315		2566	247	
SE+		21.2**	1022.6**		174.8**				
CV%		79			77			79	

*, ** and *** statistically significant at 0.05, 0.01 and 0.001 level of significance, respectively.

Values in parentheses are SEs. Source: Rupela *et al.* (2006).

However, differences in microbial numbers and activity were not as great (Table 7). The composition of the soil biota apparently has more bearing on crop performance than do aggregated measures. Total numbers of bacteria and fungi in the soils of SRI and control plots were not much different. However, mean microbial biomass carbon (MBC) was 2–41% higher for SRI in three of the four seasons, even if differences were not statistically significant because of their wide variability (Table 7). The numbers of certain microbial species – phosphate solubilizers and siderophore producers which help plants acquire Fe – were higher in SRI plots, but again the differences were not statistically significant.

Three differences between the two sets of plots were significant at the 0.01 level of confidence: numbers of N fixing bacteria, microbial biomass nitrogen (MBN), and levels of dehydrogenase (Table 7). The dehydrogenase enzyme which oxidizes a substrate by transferring one or more

hydrides [H⁻] to an acceptor, usually NAD⁺/NADP⁺ or a flavin coenzyme such as FAD or FMN, is considered to be an indicator of the level of life in the soil. Total N and total P as well as available P were also higher in SRI plots, although these differences were not statistically significant.

One of the confounding factors in this study's analysis was that it combined the results from both rainy and post-rainy seasons. Soil conditions in the latter are more aerobic and thus quite different from the former, the more so because in the rainy season many farmers were not able, or did not try, to control and limit their water applications as recommended. Yields in all four seasons were higher from SRI plots, and this difference was statistically significant. SRI yields ranged from 6.91–8.21 t ha⁻¹ compared to 5.39–6.75 t ha⁻¹ under conventional management. However, the 22–28% increases observed were less than reported from a number of other SRI evaluations, such as that in eastern Indonesia with 12,133 on-farm comparison trials which reported a 78% average increase (Sato & Uphoff, 2007).

Table 7. *Properties of soil samples from SRI and control rice plots at fields of selected farmers in Andhra Pradesh, India, during four seasons (post-rainy 2004/05 to rainy 2006)*

Parameter	SRI	Control*	SE+	CV (%)
Bacteria (log ₁₀ g ⁻¹ dry soil)	6.15	6.18	0.044 NS	1.4
Fungi (log ₁₀ g ⁻¹ dry soil)	4.35	4.35	0.029 NS	1.3
Siderophore producers (log ₁₀ g ⁻¹ dry soil)	4.48	4.33	0.117 NS	5.3
Phosphate solubilizers (log ₁₀ g ⁻¹ dry soil)	3.40	3.28	0.154 NS	9.2
<i>Pseudomonas fluorescens</i> (log ₁₀ g ⁻¹ dry soil)	4.20	4.20	0.035 NS	1.7
N ₂ -fixers (log ₁₀ g ⁻¹ dry soil)	4.47	4.20	0.020**	0.9
Microbial biomass carbon (mg kg ⁻¹ soil)	1242	1187	58.1 NS	9.6
Microbial biomass nitrogen (mg kg ⁻¹ soil)	30	25	0.7**	4.9
Dehydrogenase (µg TPF g ⁻¹ 24 h ⁻¹)	114	93	3.0 **	5.7
Total N (mg kg ⁻¹ soil)	1082	1050	15.0 NS	2.8
Total P (mg kg ⁻¹ soil)	589	545	5.7 NS	2.0
Available P (mg kg ⁻¹ soil)	20.2	17.8	0.60 NS	6.3
Organic carbon (%)	1.06	1.06	0.002 NS	0.3

* Mean from plots where farmers used their usual practices. ** = Significant at 0.01 level of significance, NS = Not significant. Source: Rupela *et al.* (2006).

Researchers at the Agricultural University of Bogor (IPB) in Indonesia have been doing a number of soil biology studies evaluating SRI crop management, including greenhouse gas emissions from SRI vs conventional plots. Of relevance here are results that show significant differences in the numbers of beneficial bacteria in the rhizospheres of plants when SRI practices are used, especially with organic fertilizers. Replicated treatments were compared for conventional rice production using NPK fertilizer; SRI practices using NPK fertilizer; SRI practices with organic fertilization (compost); and SRI practices applying NPK plus a bio-organic fertilizer¹.

The comparisons in Table 8 show that the total population of bacteria in treatment plots doubled with the combined effect of inorganic and organic fertilization, and that organic fertilization produced a population two-thirds higher than with application of inorganic fertilizer. Specifically, organic fertilization with SRI practices contributed to almost four times more *Azospirillum*, and almost doubled the number of *Azotobacter* and phosphobacteria.

¹The biofertilizer used was FERTISMART, which is commercially available and is advertised as containing rock phosphate and dolomite (calcium magnesium carbonate), plus large numbers of beneficial bacteria (*Azotobacter*, *Azospirillum* and *Aspergillus niger*).

Table 8. Total microbes and numbers of beneficial soil microbes (CFU g⁻¹) under conventional and SRI rice cultivation methods at Tanjung Sari, Bogor district, Indonesia, Feb–Aug 2009

Treatments	Total microbes (×10 ⁵)	<i>Azotobacter</i> (×10 ³)	<i>Azospirillum</i> (×10 ³)	PSM (×10 ⁴)
Conventional (T0)	2.3a	1.9a	0.9a	3.3a
Inorganic SRI (T1)	2.7a	2.2a	1.7ab	4.0a
Organic SRI (T2)	3.8b	3.7b	2.8bc	5.9b
Organic SRI + BF (T3)	4.8c	4.4b	3.3c	6.4b

CFU = colony forming units PSM = Phosphate-solubilizing microbes BF = Bio-organic fertilizer
 Values with the different letters in a column are significantly different by LSD at the 0.05 level.

Treatments: T0 = 20 cm × 20 cm spacing, 30 day seedlings, six seedlings/hill, 5 cm flooding depth of water, fertilized with inorganic NPK (250 kg urea, 200 kg SP-18, 100 kg KCl ha⁻¹); T1, T2, T3 = All 30 cm × 30 cm spacing, 6–10 day seedlings, 1 seedling/hill, moist soil or intermittent irrigation, with different fertilization: T1 = same inorganic NPK as T0; T2 = 5 t ha⁻¹ of organic fertilizer (compost); T3 = same inorganic NPKI as in T0 + 300 kg ha⁻¹ bioorganic fertilizer. Source: Iswandi *et al.* (2009).

Such numbers will certainly vary from one set of trials to another because of soil, climate and other factors, so many more such evaluations should be done to gain a better understanding of the factors that affect bacterial population dynamics in conjunction with crop, soil, water and nutrient management variables. But it does appear that a major factor contributing to positive SRI crop results is that its practices, respectively and taken together, create conditions in which beneficial soil microbes prosper. And as they thrive, so do rice plants.

Possible Contributions of Beneficial Endophytes

An advantageous correlation was seen in Table 2 between *Azospirillum* inhabiting rice plant roots – affected by crop, soil, water and nutrient management practices – and associated rice yields. This first finding alerted us to the fact that symbiotic microbial endophytes are not limited to legumes, but can also be seen in rice. Research in Egypt showed in more detail that when soil rhizobia inhabit rice roots, this increases both grain yield and the protein content of grain (Yanni *et al.*, 2001; Dazzo & Yanni, 2006). The exact mechanisms remain unclear, however. The simplest explanation that comes to mind, that microbial N fixation is occurring, is not supported by the evidence generated thus far.

Research in which Dazzo & Yanni (2006) collaborated with Chinese colleagues has taken this line of study further. It throws new and revealing light upon the subject of positive plant-microbial interactions. Feng *et al.* (2005) have documented the migration of soil rhizobia up the roots and stems of rice plants to locate themselves in the leaves, in other words, moving up from the rhizosphere to the phyllosphere, reaching populations as high as 9 × 10¹⁰ rhizobia per cm⁻³ of infected host leaf tissue.

Five different strains of soil rhizobia were evaluated under controlled conditions, comparing presence *vs* absence of certain bacteria in the plant leaves. Compared with plants that had no soil rhizobia in their leaves, those rice plants whose leaves were inhabited by rhizobia had significantly greater root volume, dry weight of shoots, net photosynthetic rate, water utilization efficiency, larger flag leaf area, and higher grain yield (Table 9). The average yield per pot was 50% higher from rice plants that were ‘infected’ by soil rhizobia compared with plants not hosting these bacteria in their leaves.

The multiplicity of positive effects associated with these symbiotic endophytes gives force to the growing interest in epigenetics as a field of study, to understand better the conditions and mechanisms for inducing certain (especially favorable) expression of genetic potentials. In

this case, we are interested in their impact on root and shoot growth, photosynthesis, and more productive use of water, all contributing ultimately to greater production.

No evaluation was done of leaf endophytes in the evaluation of SRI effects reported by Thakur *et al.* (2009). But this research documented a net photosynthesis in plants of the same rice variety almost 2× as high when grown with SRI cultural methods ($23.15 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared to the growing of it with management practices recommended by the Central Rice Research Institute of India ($12.23 \mu\text{mol m}^{-2} \text{s}^{-1}$). Further, the transpiration rate in the SRI phenotypes was 16% lower ($6.41 \text{mmol m}^{-2} \text{s}^{-1}$) compared to phenotypes grown with conventional practices ($7.59 \text{mmol m}^{-2} \text{s}^{-1}$).

A higher ratio of photosynthesis rates compared to transpiration rates indicates that SRI phenotypes were using water more efficiently than conventional plants, producing $3.6 \mu\text{mol}$ of CO_2 fixed per mmol of water transpired, compared to $1.6 \mu\text{mol}$ of CO_2 fixed per mmol of water transpired. This represents 125% greater water use efficiency and higher water productivity in absolute terms. Knowing what we now know from the research of Feng *et al.* (2005), it would be worth examining what symbiotic endophytic processes might be occurring within SRI plants which support epigenetic influences that could be producing more productive phenotypes from the same genotypes.

Table 9. *Effects of endophytic soil rhizobia migrating into rice plant leaves*

Rhizobium test strain	Total plant root volume /pot (cm^3)	Shoot dry weight/pot (g)	Net photo-synthetic rate ($\mu\text{mol}^{-2} \text{s}^{-1}$)	Water utilization efficiency	Area of flag leaf (cm^2)	Grain yield/ pot (g)
Ac-ORS571	210 ± 36^A	63 ± 2^A	16.42 ± 1.39^A	3.62 ± 0.17^{BC}	17.64 ± 4.94^{ABC}	86 ± 5^A
SM-1021	180 ± 26^A	67 ± 5^A	14.99 ± 1.64^B	4.02 ± 0.19^{AB}	20.03 ± 3.92^A	86 ± 4^A
SM-1002	168 ± 8^{AB}	52 ± 4^{BC}	13.70 ± 0.73^B	4.15 ± 0.32^A	19.58 ± 4.47^{AB}	61 ± 4^B
R1-2370	175 ± 23^A	61 ± 8^{AB}	13.85 ± 0.38^B	3.36 ± 0.41^C	18.98 ± 4.49^{AB}	64 ± 9^B
Mh-93	193 ± 16^A	67 ± 4^A	13.86 ± 0.76^B	3.18 ± 0.25^{CD}	16.79 ± 3.43^{BC}	77 ± 5^A
Control	130 ± 10^B	47 ± 6^C	10.23 ± 1.03^C	2.77 ± 0.69^D	15.24 ± 4.0^C	51 ± 4^C

Values with the different letters in a column are significantly different by LSD at the 0.05 level.

Source: Feng *et al.* (2005).

Some recent research reported by Rodriguez *et al.* (2009) has shown an unexpected and very beneficial effect from having an endophytic fungus (*Fusarium culmorum*) identified in the seed coat of rice seeds. In controlled experiments where the only variable was presence vs. absence of the fungus, it was determined that when inoculated rice seeds germinated, they produced five times more root growth. Fig. 4 shows the ratio of root: shoot growth over the first 5 days after germination, and arrows indicate when the growth of root hairs began during this period.

These authors' research on sagebrush (*Artemisia* sp.) speciation, reported in this same article, showed how dependent different plant species are on their own respective species of fungal root symbionts. Indeed, it appears that all plants in natural ecosystems are beneficiaries of symbiotic relationships with fungal endophytes (Rodriguez *et al.*, 2008).

While the field of epigenetics has focused largely on molecular biology, tracing for example the effects of methylation of DNA segments of the genome, perhaps its purview should be extended to encompass biological and ecological phenomena along with molecular biochemistry,

to examine the epigenetic effects of inter-species associations in agricultural systems. Beyond studying the positive effects of plant-microbe interactions, scientists should be engaging with parallel relationships in the realm of fauna, as is being proposed for study under the rubric of meta-genomics (Singer, 2007).

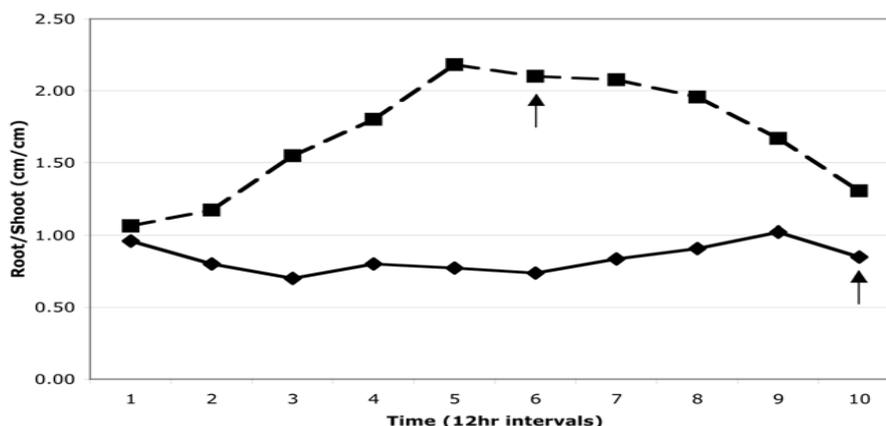


Fig. 4. Ratio of root to shoot growth in symbiotic and nonsymbiotic rice plants during the first 5 days after germination. The upper line (square marks) is for symbiotic plants inoculated with *F. culmorum*; lower line (diamond marks) is for nonsymbiotic plants. Arrows indicate initiation of root hair emergence. Source: Rodriguez *et al.* (2009).

There are already some promising investigations within the realm of plant science which we think are relevant to explaining the phenomena presented by SRI. Certain effects documented with tomatoes (*Lycopersicon esculentum*) – where mulching the plants with a leguminous cover crop rather than black plastic mulch, and applying less rather than more inorganic N fertilizer, resulted in healthier plants and higher yields – could be traced to hormonal signaling between roots and shoots which resulted in beneficial gene expression (chitinase, osmotin, chaperone production) or blocked detrimental expression (pro-senescence genes) (Kumar *et al.*, 2005; Mattoo & Abdul-Baki, 2006; Mattoo & Teasdale, 2009). This kind of genetic activity could be happening in rice plant canopies in response to altered conditions in the roots and root zones, with microorganisms playing an active role. Microbes may not be passive by-standers while plants, on their own, control multiple genetic and physiological processes.

The association between plants and mycorrhizal fungi is apparently more complicated than the previous understandings of how these endophytes benefit their plant hosts. It has been easy to imagine how these specialized fungi through their hyphae which they extend into the soil would absorb water and solubilize P and other nutrients which would then be ‘pumped’ into the root and shared with the plant. This ‘hydraulic’ concept of the symbiotic relationship is apparently too simple and an insufficient explanation since much more is going on in plant roots when inhabited by mycorrhizal fungi.

Smith *et al.* (2003) investigated the relative contributions of direct and indirect uptake mechanisms for different plants’ roots with respect to soil P, respectively through the root epidermis and root hairs or through mycorrhizae. It was found that inoculation of plant roots with arbuscular mycorrhizal (AM) fungi did not always increase plants’ growth but this did not mean that fungi were not relevant or active.

Indirect pathways (mycorrhizae induced by inoculation) were seen to substitute often for direct ones. Roots that were hosts to AM fungi underwent significant changes in the functioning of their epidermis (outer cell layer) and hair roots, with down-regulation of the expression of P-transport genes, so these other pathways for P uptake became less operative, superseded by the functioning of fungal hyphae. These findings suggest that the associations between plant roots and fungal endophytes are much more complicated and more intimate than implied by the common

understanding of how mycorrhizal fungi operate, acquiring and translocating water and nutrients from the soil environment into roots.

Soil organisms produce a significant share of the phytohormones that regulate and accelerate plant growth and otherwise originate from plant cells (Frankenberger & Arshad, 1995; Khalid *et al.*, 2006). While phytohormones appear to be more involved in physiological processes than epigenetics, the line between these intellectual domains is likely to become blurred as we delve more deeply into the realm of gene expression, building bridges between molecular biology and higher-level relationships in the biology and ecology of organisms, and moving from the roots to the top of the metaphorical ‘tree of life.’ Perhaps its ‘branches’ are better conceived in terms of nested concentric circles, extending from a prokaryotic center to a vast proliferation of eukaryotic life with no real periphery. Smith *et al.* (2003) suggest that more collaboration among physiologists, molecular biologists, and ecologists is needed.

A Negative Result

The interactions among species in a functioning ecosystem are likely to be positive only on balance, and over time. Many interactions are negative for at least some of the participants in these interactions, and for some periods the net balance can be negative. With SRI management, not all of the organisms in, on and around plant roots are necessarily or always beneficial.

In at least one area we know that the introduction of SRI methods did not produce superior results: northern Thailand (Gypmantsiri, 2002; Sooksa-nguan *et al.*, 2004). Sooksa-nguan, when examining the soil in her trial plots, found that root-feeding nematodes were thriving under the more aerobic soil conditions of SRI water management, so they were reducing crop yield.

There should be some way that SRI paddies in that region can be intermittently flooded, enough to suppress these soil herbivores. But this report was a reminder that taking an ecological perspective requires casting one’s mental net widely. Many observed effects are contingent on multiple concurrent influences, and cannot be properly understood in terms of one or two causes (Coleman *et al.*, 2004).

Discussion

There is a natural tendency to pay particular attention to causal factors that can be seen and easily measured. The common practice of sterilizing or fumigating soil samples so that their analysis is done under axenic conditions -- without interference or influence of soil organisms -- is unwittingly pernicious. The root of this adjective (a-xenic, not xenic) derives from the Greek word *xenos*, which means foreigner or stranger. The word thus implies, even if it does not say this explicitly, that soil organisms – reduced to inert organic matter by heating or chemical means for the sake of having more replicable results – are to be regarded as creatures that do not belong in their own habitat! (Uphoff *et al.*, 2006).

The plant-microbial associations and interactions related to SRI crop management practices are difficult to see and often even to conceptualize so they are easy to overlook unless special and often strenuous efforts are made. The results that synergistic use of SRI practices can achieve – producing the kind of rice plant shown in Fig. 5 on the next page, with 223 fertile tillers coming from a single seed – should make ignoring these associations and interactions more difficult in the future.

Research on these relationships is still in its early stages. But there is enough evidence, and tentative explanations are already available, that biological scientists who are working on such relationships in other contexts should be interested and intrigued. Advances in knowledge derived from SRI experimentation and evaluation could have some quick and very significant results for the benefit of humankind as we proceed in this century with both continually growing demand for food and growing uncertainty and unpredictability of climate (Uphoff, 2010).

Gaining more understanding of the mechanisms associated with SRI cultivation methods, and of their rates and limits, will contribute to more productive and sustainable agriculture. However, comprehending the effects of SRI methods will be a challenge to those who normally undertake their research based on reductionist approaches, preferring to examine the main effects of just one or two variables at a time (Stoop *et al.*, 2009). SRI research and evaluation requires more comprehensive approaches and a deeper understanding of the biology of ecosystems.

Many positive soil-plant-microbial interactions are known to occur within production systems now grouped under the rubric of Conservation Agriculture (CA) (Friedrich *et al.*, 2009). These keep soil disturbance to a minimum and maintain soil cover along with rotation of crops, practices that conserve the soil and enhance its microbial communities and their habitats. They sustain belowground biodiversity and enable the soil biota to perform its beneficial productivity-enhancing and fertility-sustaining functions. In CA systems, direct seeding is the norm, whereas SRI methods were developed with transplanting as the mode of crop establishment. However, these bodies of knowledge and practice can converge because they are based on similar agroecological and soil biological principles and insights.

It appears that by extending what is being learned from SRI experience with irrigated rice to rainfed production, to other crops, and to CA production systems generally (Uphoff & Kassam, 2009), substantial gains can be made in crop productivity, water saving, enhancement of soil and water quality, and poverty reduction based on positive plant-soil-microbial interactions.



Fig. 5. Stump of rice plant (cv. Ciherang) grown from a single seed using methods of the System of Rice Intensification (SRI), by farmers trained in SRI methods by the corporate social responsibility program of Sampoerna PT, in Pandaan, East Java, Indonesia. Presented by farmers to N. Uphoff, 6 Oct 2009. The plant produced 223 fertile tillers, which means that it had reached the 14th phyllochron of growth before vegetative growth was replaced by grain reproduction. Photo by N. Uphoff.

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