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Rethinking the concept of 'yield ceiling' for rice: implications of the System of Rice Intensification (SRI) for agricultural science and practice[1]

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The System of Rice Intensification (SRI) developed in Madagascar in the early 1980s shows promise for substantially raising rice yields on a large scale from their present world average of 4.3 tons per hectare, while also offering a number of environmental benefits. There was already by 2002 considerable evidence of this (Uphoff *et al.* 2002; Stoop *et al.*, 2002),[2] and this evidence has continued to accumulate since (Mishra *et al.*, 2006; Ghosh *et al.*, 2009 Stoop 2011; Uphoff 2011; Uphoff 2012). When SRI methods are used skillfully, improving soil fertility as a consequence of optimizing management of rice plant seedlings, soil, water and nutrients, yields are generally higher, and maximum yields in the range of 15 to 20 t ha^{-1} have been reported, and occasionally even higher.

According to Virk *et al.* (2004), the yield potential of irrigated rice crops in the tropics increased from 6 to 10 t ha^{-1} during the 1960s. This was accomplished primarily by breeders at the International Rice Research Institute (IRRI) and elsewhere reducing plant height through the incorporation of a recessive gene (sd1) for short stature from a Chinese variety Dee-geo-woo-gen. According to Khush (1995), the yield potential of IR8 during the *dry season* in the tropics when it was released in 1966 was about 9.5 t ha^{-1}. However, it now yields about 7.5–8.0 t ha^{-1} under best management practices, while several subsequent IR varieties have outyielded IR8 by 15–20% (Virk *et al.*, 2004).

In the late 1980s, IRRI proposed development of a New Plant Type (NPT) highlighted in its 1989 strategic plan with a yield potential 20-25% higher than that of the existing improved semi-dwarf varieties of rice in the tropical environment during the dry season (Peng *et al.*, 1994; Khush 1995; Conway 1997; Virk *et al.*, 2004).[3] As it has turned out, we have seen farmers using SRI crop management methods often achieving yields higher than were predicted for the NTP, even during the wet season in tropical environments.

***Note*:**

1. *This article was originally written in 2002 but not published then because the data available on SRI were not yet sufficient for publication in the peer-reviewed literature. It has been updated or publication now because the issue it addressed -- 'yield ceiling' -- has been revived by controversy over the reported world-record yield in Bihar state of India. References here to literature that was available at the time (2002) and my discussion thereof show how much was known and documented more than a decade ago about processes and effects that could help to explain remarkable increase in rice yield with SRI management methods. This article was focused entirely on SRI as applied to irrigated rice production. We had no knowledge then of applications to rainfed rice and other crops.*

2. *Early evidence of SRI productivity came from cooperation between Association Tefy Saina, the NGO in Madagascar most actively promoting SRI, and the Cornell International Institute for Food, Agriculture and Development (CIIFAD) working in the peripheral zone around Ranomafana National Park under a USAID-funded project to protect rainforest ecosystems there. Tefy Saina and CIIFAD sought to help farmers raise their rice yields and reduce their shifting cultivation that was destroying forests. The number of farmers using SRI methods went from 38 in 1994-95 to 395 in 1998-99. SRI yields with average yield over 8 t ha^{-1}, compared with the 2 t ha^{-1} yields that farmers got with conventional practices in the area and in the country at large (Uphoff 1999). During this same period, farmers using SRI practices on the high plateau of Madagascar, cultivating over 500 ha of rice in small-scale irrigation systems being upgraded with French assistance, averaged 7.91 t ha^{-1} around Antsirabe and 9.18 t ha^{-1} around Ambositra. This far exceeded the 3.58 to 3.95 t ha^{-1} obtained using the technical package of high-yielding varieties, chemical fertilizer and row-planting, and the 2.24 to 2.47 t ha^{-1} with peasant practices (Hirsch 2000).*

3. *Note that IRRI has not released any NTP rice lines, and this breeding project is no longer discussed in Institute publications and reports. IRRI has since embarked upon a different genetic modification, seeking to develop rice genotypes with a C4 pathway for photosynthesis, more efficient than rice's current C3 pathway, seeking to increase the yield potential of tropical rice by another 20-25%.*

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This has raised the question: whether there is really an agronomic 'yield ceiling' for rice, and other crops, and further, if there is such a ceiling, why are farmers using SRI management methods getting rice yields greater than IRRI scientists have considered to be attainable under their recommended best practices? This focuses attention on the ecophysiological basis for the very high SRI yields reported as well as for the quite substantial differences in *average* yields that have been achieved with SRI management.

Really high yields with SRI management have been rejected by various rice scientists as impossible, being beyond the 'biological maximum' that their crop models predict -- a 'ceiling' of around 15 tons per hectare or possibly as high as 18 tons (Khush 1996; Dobermann 2004). Recent reports from India have challenged the concept of maximum biological yield. In 2012, SRI yields of 18.1 and 20.7 t ha^{-1} were reported from Tamil Nadu state of India (*The Hindu*, Jan. 19 and 22, 2013); and in the preceding 2011 *kharif* season, a yield of 22.4 t ha^{-1} was reported from Bihar state.

This latter result was challenged by Prof. Yuan Long-ping of China, whose previous record yield of 19.2 t ha^{-1} with hybrid rice had previously been considered the highest attainable rice yield (he called the Bihar yield 'a 120% fake' -- *The Hindu*, Feb. 22, 2013).

This author, reviewed data from the Bihar Department of Agriculture technicians, provided by the Indian government's Directorate of Rice Development (DRD), is satisfied that the record yield was correctly measured and reported, as explained in Diwakar *et al.* (2012). But this article is not about the controversy over record yields. Rather, it addresses questions regarding the concept and calculation of 'yield ceiling' -- and considers how what has been learned from SRI experience casts light on this subject within the framework of crop and soil sciences.

SRI remains controversial in some scientific circles. Most farmers likewise, not understanding how 'less can produce more,' have found it difficult to believe that SRI methods, using a seed rate only 10 % of what they presently use, can give them doubled yield; yet it does. By changing certain age-old ways in which rice crops are grown, it has been seen now millions of times that good use of SRI methods can increase, concurrently, the productivity of the land, the labor, and the water that farmers employ when growing irrigated rice. (And with appropriate adaptations, similar improvements can be obtained from rainfed rice.) This is a welcome but unprecedented positive-sum situation. Usually, something closer to a zero-sum situation is encountered, where any gain in the productivity from one factor must be accompanied by a reduction in the productivity from another.

Factorial trials that evaluated different combinations of SRI and conventional practices have shown how synergy among SRI practices can help to explain the positive-sum increases (Rajaonarison, 2000; Andriankaja, 2001; Uphoff and Randriamiharisoa, 2002). These appear to result from the way that beneficial biological process in soil systems and in plants are promoted by alternative management practices that require only labor and skill, not purchased inputs. As discussed below, these practices appear to be engaging the services and benefits of rice plants' microbiomes which are composed of bacteria, fungi and other organisms in the soil and in the plants (Uphoff *et al.*, 2013).

The SRI strategy of agricultural advancement is quite different from one that relies on genetic modifications and on inputs of fertilizers and other inorganic chemicals. Its effectiveness does not depend upon varietal improvement, since practically all varieties of rice thus far have responded well to the new combination of practices, recognizing that the highest yields have been achieved with 'improved' varieties. Already in Madagascar in the 1990s, the best yields with SRI practices were with varieties descended from IR-15, IR-46 and Taichung-16. So SRI results contain some good news for plant breeders.

The increased production comes in large part, we think, from greater access to and utilization of nitrogen (N), oxygen (O) and carbon (C), which are all freely available elements in the atmosphere. Soil aeration, both passive and active, makes N and O more available in the rhizosphere and in the rice plants themselves. This enhances the magnitude, complexity and diversity of communities of organisms living in, on and around the plants' roots and leaves. As the same time, soil aeration and other SRI practices support the greater capture of atmospheric C through improved photosynthesis and the growth of larger, healthier plant root, while enhancing the release of deleterious gases (CO_2 and H_2S) from the soil.

Diverse organisms can improve soil quality in many ways, particularly enhancing soil aggregation and porosity, thereby making the soil more water-retentive. Better-structured soil is more friable and penetrable for better root growth and performance. Microorganisms can contribute to agricultural productivity through biological nitrogen fixation (BNF) and microbially-mediated processes like phosphorus solubilization (Haygarth and Turner 2001), probably mobilizing various micronutrients as well.

Alternating aerobic and anaerobic soil conditions as occurs with SRI water management and weeding practices contributes to these dynamics. There is long-standing evidence that alternate wetting and drying of soil can increase the level of BNF substantially (Birch 1958; Magdoff and Bouldin 1970). Modified soil-water management can also make other contributions to plant nutrition and growth, e.g., by permitting the growth and functioning of mycorrhizae. These fungal phenomena cannot survive under the anaerobic conditions of continuously flooded soil; thus they are not common with standard paddy rice management and are little studied (exceptions include Ilag *et al.* 1987 and Solaiman and Hirata 1997). When rice plants are kept flooded, they forgo the benefits that mycorrhizal 'infection' confers on most terrestrial plants.

SRI plants are visibly larger in size, produce greater crop biomass weight per unit area (and this can only occur with higher net photosynthesis rate), and their components of yield per unit area are greater: number of effective (grain-bearing) tillers, number of spikelets per panicle, number of grains per spikelet, and heavier individual grains. SRI crops thus have different phenotypic expression of genetic potential in terms of their phenology and their below- and above-ground' morphology, as well as their growth and yield physiology (Thakur *et al.*, 2010).

Ten years ago, relatively little was known about the various contributing factors to SRI performance. Much still remains to be investigated with scientific methods. However, agronomic and physiological knowledge about SRI has moved on many fronts beyond hypotheses, as seen from the almost 400 journal articles and many other publications now posted on the SRI-Rice (website: http://sri.ciifad.cornell.edu/ research/index.html).

Much remains unknown about the contributions that the soil biota make to SRI performance; however, this area of knowledge is starting to be defined and refined (e.g., Randriamiharisoa *et al.*, 2006; Anas *et al.*, 2011; Lin *et al.*, 2011). Such knowledge will be essential for a fuller understanding of SRI results and impacts. Here the focus is on understanding the 'yield ceiling' issue and considering where revisions in conventional rice science thinking could accordingly be usefully made.

The System of Rice Intensification

This methodology for growing rice has been described in several early publications (Laulanié, 1993; Uphoff ,1999; Uphoff, 2002; Stoop *et al.*, 2002). Its initial formulation was summarized in terms of six practices. The first four practices represented departures from conventional methods and called for scientific investigation; the latter two were not particularly controversial, but there was some question about how many farmers would adopt these more labor-intensive practices. In fact, even though SRI requires more time and effort initially while the new methods are being learned, the system becomes attractive when farmers can see its results and begin to understand it, because it gives them higher returns to labor as well as other inputs (Anthofer, 2004; Sinha and Talati, 2007). Unless rice production has been previously very extensive with little labor input made per hectare, SRI methods will usually become labor-saving once they are learned.

The main elements of SRI are:

a) *Transplanting young seedlings*, *just 8-15 days old*, instead of seedlings that are 21 days or older, because this preserves plants' tillering and root-growth potential that is lost by transplanting seedlings after the start of their fourth phyllochron of growth, discussed below. These should be grown in an unflooded, well-drained nursery for best root growth and health.
b) *Transplanting seedlings singly*, rather than in clumps of 3 or more plants, and *widely spaced*, in a square pattern, usually 25x25 cm (although possibly 20 x 20 cm on poorer soil, or even more widely if good soil conditions make this optimal). Such wide spacing provides more room for greater growth of roots and canopies.
c) *Transplanting the plants carefully* so that they suffer little or no trauma and can quickly resume their growth. Roots are treated carefully so that they do not become desiccated or traumatized.
d) During the plants' vegetative growth phase, *the soil should be moist but well-aerated*, either through light, intermittent irrigation, or by alternately flooding and drying the soil for 3-5 day periods. In either case, continuous flooding is avoided as this creates hypoxic soil conditions. After panicle initiation, once the reproductive phase begins, a thin layer of water, 1-2 cm, is maintained until 10-20 days before harvest.
e) *Weeding 2 to 4 times before canopy closure*, starting 10 days after transplanting, preferably with a simple mechanical weeder (rotating hoe or cono-weeder) that aerates and loosens the soil for better root growth at the same time that it controls weeds, burying them in the soil.
f) *Application of compost* to the soil before planting. Chemical fertilizer can also give good results with SRI; but in conjunction with the other practices, compost has given better yields by building up the soil's organic matter and microbial activity.

While SRI was developed for transplanted, irrigated rice, in a number of areas where rice production is unirrigated and relies on rainfall, adaptations are being made to capitalize on the benefits of wider spacing and soil aeration, by establishing the crop through *direct seeding*, which saves labor time. SRI is usually best suited to households with small holdings, who have the labor supply and the incentive to cultivate more intensively.

However, mechanization of transplanting and weeding to reduce labor requirements is being undertaken in some areas so that SRI can be adapted for larger-scale production.

'Yield ceiling' has been assessed previously under suboptimal growth conditions

It has been proposed that further production increases are constrained by a physiological 'ceiling' set by the present genetic potential of rice plants (Khush, 1996; Khush and Peng, 1996). After impressive progress during the first years of the Green Revolution, gains from high-yielding varieties have slowed down and even stagnated. Per capita cereal production peaked in the mid-1980s, and total cereal production has not increased since the mid-1990s. The hybridization of rice in China has contributed to further yield increases by utilizing the positive effects of heterosis, but yield gains with this strategy too have essentially plateaued (Li and Yuan, 1998). It is true that some further increases in yield could have been achieved if grain prices had been higher, justifying greater expenditure on inputs. But this would make achieving food security for the billion people who are still living in hunger even more difficult (Conway, 2012).

The results achieved with SRI practices challenge the idea that there is a 'biological maximum yield' for rice which has been reached and can best, or only, be transcended by changing the rice genome through breeding improvements, or changing its photosynthesis pathway from C3 to C4. SRI plant and crop management practices show, instead, that there is still substantial yield potential in rice that can be tapped agronomically by altering the growing conditions for rice plants. The proposed 'ceiling' appears to be an artifact of current crop management practices and thinking.[4]

As noted above, the highest yields with SRI methods so far have been achieved with 'modern,' i.e., genetically improved varieties. So management and genetic modification should not be viewed as alternative approaches. However, there are differences in emphasis and priority. Advances in plant breeding are less seminal if changes in management can achieve the same objectives more quickly and inexpensively.

Estimating a biological ceiling is necessarily an inexact process, since one must deal with varietal differences and different responses to particular growing conditions. It has been thought previously that the maximum attainable yield is between 12 and 15 t ha^{-1}, although in practical terms, it appears to be lower. Ladha *et al.* have noted that "Yields for multiple varieties peak out at about 8 t ha^{-1}, even with high nitrogen applications, up to 200 kg ha^{-1}" (1998: 60-61).[5]

***Note*:**

4. *Ideas about a fixed 'yield ceiling' appear to derive from the concept of plant ideotype as proposed and defined by Donald (1968). This is an idealized plant type with a specific combination of characteristics that are considered favorable for photosynthesis, growth, and grain production, based on current knowledge of plant and crop physiology and morphology. This thinking encouraged crop breeders to define a plant type that was theoretically most efficient and then to breed for this ideotype (Hamblin 1993). Such a 'blueprint' approach to breeding toward standard ideotypes for their suitability under some fixed, standardized agronomic and water management practices led rice scientists to posit a fixed yield ceiling to be transcended.*

Yield is an end result of the phenotypic expression of crop plants' genetic potential, based on a complex set of Genotype x Environment x Management interactions. The estimation of a fixed, maximum-attainable crop yield is thus rather tenuous, especially when it is calculated from models of plants that exclude consideration of their roots' status and performance (footnote 13). Additionally, much of crop physiological thinking has been conditioned by the notion that there is not much scope for changing the unit rate of photosynthesis (Evans 1993), and with it for improving crop growth or biomass production per unit area. Instead, what could be changed to increase crop yield was the Harvest Index: the proportion of total crop biomass that ends up in the crop's edible portion. Within such a construct of fixed/zero-sum rice agronomy, plant breeders, agronomists and physiologists have been conditioned to thinking that yield improvements must come from genetic traits that control the Harvest Index.

5. *As discussed more below, researchers have focused primarily on the supply of nitrogen (N) and its uptake by the plant as the critical factor in raising rice yields. Kronzucker et al. (1999: 581), citing Cassman et al. (1997), have written: "Nitrogen is generally the main factor limiting the realization of yield potentials." Along these lines, Ladha et al. (1998: 41) advise that: "To increase grain yields, additional nitrogen must be applied as fertilizer" (1998: 41), emphasis added in both citations.*

With the expectation that greater N applications are the major requirement for increasing grain yield, it is easy to understand why scientists have rejected reports of SRI yields reaching 15 to 20 t ha^{-1}, and even more emphatically when no chemical fertilizers have been applied, only compost or other organic matter. No consideration is given to the possibility that high N applications along with other 'modern' practices may actually *constrain* yield by affecting the soil biota (more on this below). One can find in the rice science literature a number of reasons why present estimates and explanations for a 'yield ceiling' have been misconstrued.

Present management practices and thinking contribute to suboptimal yields

Arguments supporting the concept of a 'biological maximum yield' have been based on rice-growing practices and assumptions *that themselves limit production*, as seen below. The following statements, which contradict present management practices and assumptions, are supported by a variety of research findings, discussed in following sections.

- *Rice plants that are planted densely and are grown under continuously flooded conditions, as currently thought to increase yield, will have less root growth and also more root degeneration.* These effects necessarily impair rice plants' functioning and their eventual yield. *Conventional transplanting practices traumatize seedlings and diminish both root growth and associated tillering. These practices set back the plants' growth and eventual yield, particularl*y if the seedlings are relatively mature when transplanted. This effect is explainabl*e in terms of phyllochrons' influence on rice growth patterns.*
- *Efforts to induce greater plant growth by providing them with ever-larger supplies of inorganic nutrients, especially synthetic N, overlook the fact that nutrient uptake by rice roots is a demand-driven process* (Kirk and Bouldin 1991). The current approach to plant nutrition, which has been fixated more on the *supply* of nutrients than on plants' *demand* for them, contributes to the low nitrogen-use efficiency that is observed with irrigated rice, only 20-35%, according to Ladha *et al.* (1998).

Before considering the support for these three statements that can be found in the rice science literature, we should consider some important phenotypical differences in the rice plants that regularly result from SRI practices.

Phenotypical manifestations with SRI practices contradict 'yield ceiling' thinking

While exact levels of yield with SRI practices will vary according to soil, climatic and varietal effects, as well as with the skill with which the practices are used, three evident changes in the structure and performance of rice plants are associated with SRI methods. This variability suggests that highest attainable yield would not be a consequence primarily of a fixed genetic potential that is implied by 'yield ceiling' calculations. These changes have been measured and are easily observable by farmers or anyone else.

Rice plants grown with SRI methods have more tillers per plant, commonly 30 to 50, and as many as 80 to 100, and sometimes even more with the best use of these practices (Fig. 1). While the percentage of panicles (tillers that become fertile and bear grain) usually declines somewhat as the number of tillers goes up, there is a visible increase in the number of panicles per rice plant with SRI methods. Effective, i.e., fertile, tillering is usually in the 70-90% range.[6] To be sure, with wider spacing there are fewer plants per square meter. But with a better-developed root system (see below), there are more fertile tillers per unit area and also larger panicles, with usually higher grain weight.

Fig. 1. Rice plant (Ciherang cv.) with 223 tillers grown from single seedling with SRI methods. Presented to author by farmers at Panda'an training center in East Java, Indonesia, October 2009.

Note:

[6.] *An early SRI experiment conducted in the Philippine with rainfed SRI management, using an indigenous variety and organic fertilization, had 99% effective tillering in replicated trials (Gasparillo et al., 2003).*

Along with inducing more profuse tillering, SRI practices of wider spacing, soil aeration, etc. are seen to affect the above-ground architecture of rice plants. In controlled trials with the same variety, it was found that the tillers of SRI-grown plants were more horizontal and the leaves were more erect. Not only was leaf area index (LAI) 67% higher, but sunlight interception was 15% greater. With SRI practices also resulting in 30% higher total chlorophyll, the plants' net photosynthetic rate was raised by 89%. The leaf growth and functioning associated with greater SRI tillering thus contributed to higher plant productivity (Thakur *et al.,* 2010).

- *A negative correlation has been reported in the literature between the number of tillers per plant and the number of grains per panicle* (e.g., Ying *et al.,* 1998). However, this relationship may not be an innate characteristic of rice, reflecting 'the law of diminishing returns.[7] With SRI management, we have found there to be *a positive correlation between tillering and grain filling* (Joelibarison 1998; Bonlieu 1999; Rakotoarinoro, 2000). The number of grains per panicle is in range of 150 to 300, with some panicles having 400 or more grains. This positive relationship permitting both more tillering and more grains per panicle makes possible the larger yields measured from SRI practices.[8] What accounts for this reversed relationship are, we believe, the larger and longer-lived root systems that can result with SRI management as shown in fig. -1.
- *Root systems grow much larger with SRI practices*. Using a measure known as root-pulling resistance (RPR) -- resistance to uprooting, which reflects the number, length, diameter, branching and even surface area of roots (O'Toole and Soemartono, 1981), SRI-grown plants were found already in 1998 to have five times more RPR. Clumps of *three* rice plants grown conventionally, from mature seedlings closely spaced in flooded fields, required on average 28 kg to be pulled out of the ground, while it took, on average, 52 kg of force to uproot *single* SRI plants, immature seedlings, widely spaced, and grown in well-drained soil (Joelibarison, 1998).[9]

Rice plants that have limited root systems because of conventional flooding practices are 'closed systems,' forcing the plant into zero-sum tradeoffs between tillering and grain filling. On the other hand, plants with extensive root development become 'open systems,' allowing both tillering and grain filling to increase together. This change in root performance potential is due particularly to roots not being restricted to the top horizon of soil and not dying back, as discussed in the next section.

Further, it is evident that profuse root systems will provide for more plant interaction with microbes in the rhizosphere, making this mode of biological enhancement of crop performance more extensive. Larger root systems also support more root activity and more above-ground physiological activity as seen from measurements of increased root transport of phytophormones and other compounds for above-ground plant physiological processes (Thakur *et al.,* 2010, 2013).

These and other physical relationships observed with conventionally-grown rice compared with plants produced using SRI methods need to be accounted for. The literature offers a number of clues for why phenotypic differences occur with SRI management -- more roots, more tillering, and a positive association between tillering and grain filling.

***Note*:**

7. *If there is a negative correlation, any strategy that tries to raise rice yields by increasing the number of tillers per plant is self-defeating. This mistaken conclusion has led scientists to try to breed a "super-rice," a new plant type (NPT) that has only 8-10 tillers per plant, but with all tillers being fertile and each producing 200-250 grains per panicle (Conway 1997: 142). Such a phenotype, yet to be shown superior, contrasts structurally with that of rice (any variety) grown with SRI practices. A flaw in this plant-breeding strategy is that plants bred to have fewer tillers will also have fewer roots.*

8. *Often but not always, greater grain weight is also reported from SRI plants. The CARE program in Bangladesh found in 2000 that grain weight with SRI methods was 12 % higher compared to the weight of grains that farmers produced in its IPM farmer field schools with already-improved methods (Aziz and Hasan 2000: 5).*

9. *Early evidence of root differences came from farmers in Namal Oya, Sri Lanka, who simply compared the average root length of SRI and non-SRI rice plants. Average roots with conventional methods measured 2 inches long, while those grown with the recommended practices (fertilizer, high-yield varieties, etc.) averaged 3 inches. SRI rice roots, on the other hand, averaged 9 inches (personal communication, Gamini Batuwitage, Additional Secretary, Ministry of Lands, March 22, 2001). This might be discounted as inexact farmer measurement, but such differences are too large to be measurement error. Barison's 1998 findings were confirmed in his thesis research for a Cornell M.S. in crop science (2003) with more extensive trials and measurement. Differences in per-plant RPR between SRI and conventionally-grown rice plants were as much as 10 times, as reported in Barison and Uphoff (2011).*

- **Phenotypic observation: roots degenerate under flooded conditions**

It is not surprising that root systems will grow larger when plants are spaced more widely apart. However, for maximum rice production, one wants not just more roots but as many panicles bearing grain as possible per unit area. The approach to increasing the number of panicles per unit area has thus far been to see how *densely* rice can be planted without a decline in yield, rather than seeking a converse optimum, by evaluating *sparser* planting. Wider spacing in conjunction with the other SRI practices yields a more productive phenotype with fewer plants producing more total tillers.

Unfortunately, tillering has usually been considered separately from root growth, even though these processes are intimately associated in rice as in all other gramineae species with each tiller producing new adventitious roots at its base. Whatever inhibits root growth also constrains tillering, and vice versa, because of the way that both tillers and roots emerge from growth tissue in the plant's crown.

A larger root system can access both more nutrients and a larger variety of them. Nevertheless, in contemporary rice science, root growth is regarded more negatively than positively, even as a 'waste' of the photosynthate produced in the plant's leaves, because it lowers the *harvest index*.

It is widely believed that rice is an aquatic plant, growing well and even ideally under flooded conditions (De Datta, 1987).[10] However, when rice plants are grown under continuous submergence in water, about three-fourths of rice plant roots are still within the top 6 cm of soil one month after transplanting (Kirk and Solivas, 1997:619). It is well-known, conversely, that the roots of upland rice plants grow more deeply into their unsaturated soil.

More important, when rice is grown under flooded conditions there is significant degeneration of roots during the later phase of vegetative growth. Kar *et al.* (1974) found that by the time of panicle initiation, when rice plants were beginning their reproductive phase, 78 % of the roots on rice plants grown in saturated soil had degenerated, while there was practically no loss of roots on plants of the same variety grown in well-drained soil of the same type.

This has been known to rice scientists. Kronzucker *et al.* (1999: 1044) wrote, for example, that: "The rice root system during grain filling is subject to senescence." However, this loss of roots has not been taken seriously and assessed systematically; the research by Kar *et al.* cited above is a rare exception. This is perhaps because roots have not been considered very important, or because their loss has been viewed as natural and thus unavoidable, implied by use of the word "senescence".[11]

Rice root degeneration is, however, largely anthropogenic, a consequence of the standard water management practices used in irrigated production. This was seen from ORSTOM research which showed that both 'irrigated' and 'upland' varieties of rice formed aerenchyma (air pockets) in their roots when they were grown under flooded conditions; and *neither variety* formed aerenchyma when grown under unflooded conditions (Fig. 2) (Puard *et al.*, 1989). Rice thus is not really an aquatic plant, as generally assumed. While it can survive in standing water, it does not thrive and perform at it its best when continuously submerged. While it can adapt to hypoxic conditions, these are suboptimal.[12]

***Note*:**

[10]. *This has been the most widely cited text on rice science. De Datta says that rice "thrives on land that is water saturated, or even submerged, during part or all of its growth cycle…A main reason for flooding a rice field is that most rice varieties maintain better growth and produce higher grain yields when grown in flooded soil than when grown in nonflooded soil" (pp. 43, 297-298). This is contradicted, however, by SRI experience as well as by studies such as Hatta (1967), Ramasamy et al. (1997), and Guerra et al. (1998).*

[11.] *An indication of how little attention has been paid to roots in rice science is their neglect in the leading text on rice (De Datta, 1987). In a chapter on "the morphology, growth and development of the rice plant," out of 390 lines of text, only 8 are devoted to roots. And in the 16-page index with >1,100 entries, there are no references to 'roots.' There is one reference in the index to 'rhizosphere,' to a sentence which says only that there is a rhizosphere.*

[12.] *There are reasons to think that flooded soils are desirable for rice plant growth based on research on the chemistry of flooded soils (Sanchez (1976). But while there is enhanced availability of some nutrients when paddy soils are flooded, the uptake of nutrients still depends on the size and functioning of plant root systems, which degenerate under continuously flooded conditions. Moreover, there is little known about the net benefits of aerobic vs. anaerobic soils for rice production, considering what nutrient access and uptake benefits are lost under hypoxic conditions, such as the effects on biological nitrogen fixation (BNF) or on mycorrhizal activity.*

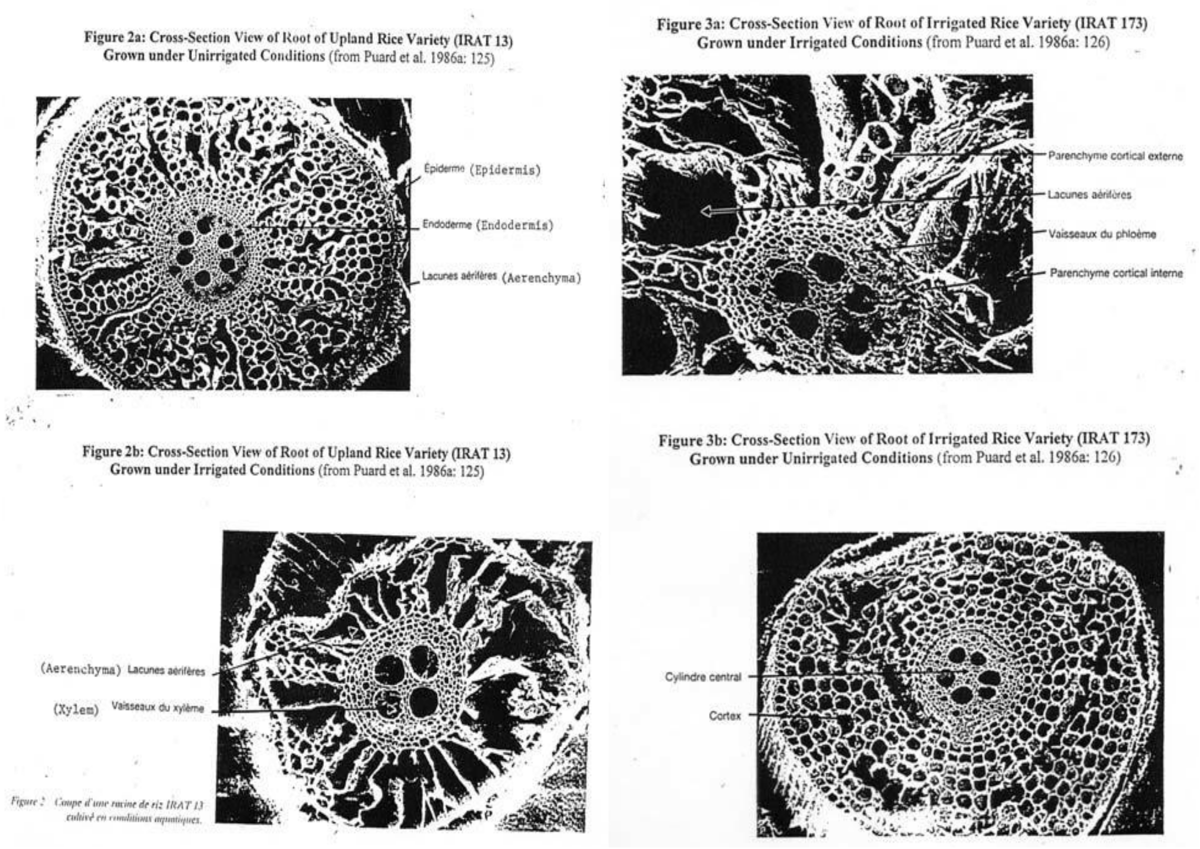


Fig. 2: Cross sections of the roots of an upland rice variety (IRAT 13) on left, and an irrigated rice variety (IRAT 173) on right, which were grown under unirrigated conditions (upper left and lower right) and irrigated conditions (lower left and upper right). Source: Puard *et al.* (1989).

Aerenchyma are formed by disintegration of cells in the roots' cortex (30 to 40%) to form spaces within the roots through which oxygen can passively diffuse to their tips. Kirk and Bouldin describe this disintegration as "often almost total" and write that it "must surely impair the ability of the older part of the plant to take up nutrients and convey them to the stele" (1991: 197). This constriction in oxygen supply contributes, by the time of panicle initiation, not just to the degeneration of root systems under submerged conditions noted above, but it will also slow the rate of tillering prior to panicle initiation (PI) and will constrain grain filling after PI when a majority of the plant's root system has become inoperative.[13]

Research has further shown that rice seedlings grown in an unflooded nursery have accelerated growth and earlier coleoptile emergence, with subsequently better growth after being transplanted at a young age (12d) into unflooded soil conditions (Mishra and Salokhe, 2008). Earlier research by Ntamatungiro *et al.* (1999) showed that grain yield correlates poorly with various plant measurements (including N content) made during the vegetative growth stage. Instead, "environmental and other conditions prevailing during later growth stages [reproductive phase] profoundly influenced the grain yield of rice.

If a plant has lost most of its root system because of hypoxic soil conditions, this will surely limit its ability to form and fill grains which, according to this research, depends mostly on "conditions prevailing during later growth stages." Moreover, research has shown that roots as plant organs do more than just take up nutrients and water to supply the canopy. They also participate in the production and transport of phytohormones and enzymes that play critical roles in plant physiology (Mishra *et al.*, 2006).

***Note*:**
[13] *Kirk and Bouldin note that after panicle initiation, "The main body of the root system is largely degraded and seems unlikely to be very active in nutrient uptake" (1991: 198). However, reflecting the standard view of rice as an aquatic or at least hydrophilic plant, they diminish the implications of this trenchant observation by adding: "Considering how well rice is adapted to growth in flooded soils…."*

The fact that rice plant roots degenerate under continuous flooding thus calls into question any calculation of a 'yield ceiling' based on previous modeling exercises to estimate the highest yield that can result when all growth parameters are at their maximum (Dobermann, 2004; Sheehy *et al*., 2004). These models are based on above-ground factors focused on leaves, such as leaf area, light exposure, temperature, and metabolic rates. With no root parameters integrated into the model, it is assumed that what occurs in plant roots has no effect on what goes on in the leaves, an untenable assumption.[14]

- **Phenotypic observation: seedlings transplanting at early age retain more potential for tillering and root growth**

This relationship can be explained with an understanding of the concept and phenomenon of *phyllochrons* as a periodicity in crop phenology. Transplanting rice seedlings from the nursery seedbed into the field is a critical management practice that precedes the vegetative growth phase. Fr. de Laulanié found this practice to have an important effect on yield. When 50 to 100 or more seedlings are being planted per square meter, it is hard to devote much time and attention to each individual seedling. Farmers who practice SRI methods in turn found that there were substantial payoffs from handling many fewer seedlings carefully, laying their roots gently into the soil with root tips oriented horizontally and shallow in the soil. Best would be to have the root tips pointed downward, but certainly not inverted upward.

Good root positioning contributes to little or no delay in the roots' resumption of their downward growth. Any days or weeks lost at the start of the plants' growth process will have large impacts on their ultimate yield since any delays postpone the start of the dramatic acceleration in tiller production that can precede panicle initiation, and delays lead to the forgoing of benefits from profuse tillering. If there is a negative correlation between tillering and the formation and weight of panicles, then slowing and reducing the rate of tillering has little adverse effect. But as seen above, with SRI management the correlation [] is positive, making tillering a desirable trait. To appreciate fully how transplanting affects tillering, one needs to understand the dynamics and effects of phyllochrons as they govern growth, discussed below.

With conventional transplanting methods, rice roots experience considerable physical trauma during nursery removal and transport [;] few efforts are made to avoid desiccation of the roots, and many of the plant's seminal roots are destroyed in the process. When seedlings are thrust down into a hypoxic soil-water environment with root tips inverted upward, it takes rice seedlings 7 to 14 days to resume their growth (Kirk and Solivas 1997: 618). What is referred to as 'transplant shock' will have a negative effect on grain production because it keeps the plant from producing as many tillers as its genetic potential could realize.

With SRI, seedlings are grown in nurseries that are managed like gardens, with well-drained, periodically-watered soil, rather than being started in flooded seedbeds. SRI seedlings are transplanted when they have only two or at most three small leaves, indicating that they have not yet begin their fourth phyllochron of growth.

Seedlings are transplanted into the field quickly, between 15 and 30 minutes after careful removal from the nursery, keeping the seed sac attached to the primary root. They should be put gently into a muddy soil environment, but not into a saturated soil that lacks oxygen. When many fewer plants per square meter are being transplanted -- 25, 16, 12, 9 or even 4 -- farmers can afford to take the time to put seedlings in quickly, carefully and deftly.

***Note*:**

14. *An early draft of Dobermann (2004) was shared with this author for comments. I pointed out that the coefficients used in the model to calculate maximum rates of photosynthesis and plant metabolism were based on measurements made from rice plants grown under continuously flooded conditions that would have diminished roots and root function compared to SRI-grown plants. So, I suggested, the calculations of the model would not necessarily apply to the less root-constrained phenotypes of rice plants grown with SRI management. This suggestion was not taken into account in that article, or in Sheehy et al. (2004). The justification given for ignoring the suggestion was that the analysis was being done for photosynthesis, and not for roots (A. Dobermann, email communication, Jan. 24, 2003).*

Transplanting tiny seedlings, only 8-15 days old, requires more care and skill, especially when spacing is done more precisely and evenly. But there are good physiological reasons for planting young seedlings in this way. Because so few seedlings are transplanted, farmers find that once they master the techniques, SRI methods require *less* labor than conventional ones.[15]

The physiological reason why careful transplanting of very young seedlings is important is that tillering is a structured, cumulative process, not simply a quantitative one as implied by the usual concepts of "low tillering," moderate tillering" and "high tillering" periods during the vegetative growth phase. Tillering proceeds according to a well-defined pattern analyzed in terms of *phyllochrons,* a patterning common to all gramineae species.

This was first recognized by the Japanese scientist T. Katayama in the 1920s and 1930s, who unfortunately could not publish his findings until after World War II. Even more unfortunate, his book (1951) has never been translated into English, so plant scientists in the West have little acquaintance with this concept. In recent years it has become more widely known among wheat and forage scientists, but not yet among many rice scientists.[16]

The significance of understanding *phyllochrons* for increasing rice production has been discussed in Laulanié (1993; also in Uphoff 1999, and Stoop *et al.,* 2002). Here it is noted that there will be greater trauma to rice seedlings if they are transplanted after the end of their third phyllochron of growth, usually about 15 days after seedling emergence depending on temperature and other conditions (Nemoto *et al.* 1995). If the plant experiences trauma after its primary tillering begins, its growth trajectory will be slowed, and the plant is less likely to complete more than 8 phyllochrons of growth before its reproductive phase begins after concluding its prior phase of vegetative growth, instead of reaching 10, 12 or even more.

Phyllochrons are variable periods of plant growth observable in all gramineae species. Each phyllochron is a period, or cycle, of tiller, root and leaf formation, for rice usually lasting between 5 and 8 days according to climatic, soil, varietal and other influences (Nemoto *et al.,* 1995). With ideal conditions it could be a short as 4 days, or with conversely unfavorable growing conditions, it could be 10 days or more.

In each phyllochron, first one and then successively more phytomers (units of a tiller, a leaf and a root) are produced from the plant's ground-level apical meristem. If a plant can go through 11 or 12 phyllochrons of growth before it flowers and commences its reproductive phase, dozens of phytomers (units of tiller, leaf and root) can be produced in a single cycle of growth. A rice plant that completes only 7 or 8 phyllochrons before flowering will have only 8 to 13 tillers, whereas one that completes 12 phyllochrons before panicle initiation can have 84 tillers. There is a corresponding increase in the number of roots.[17]

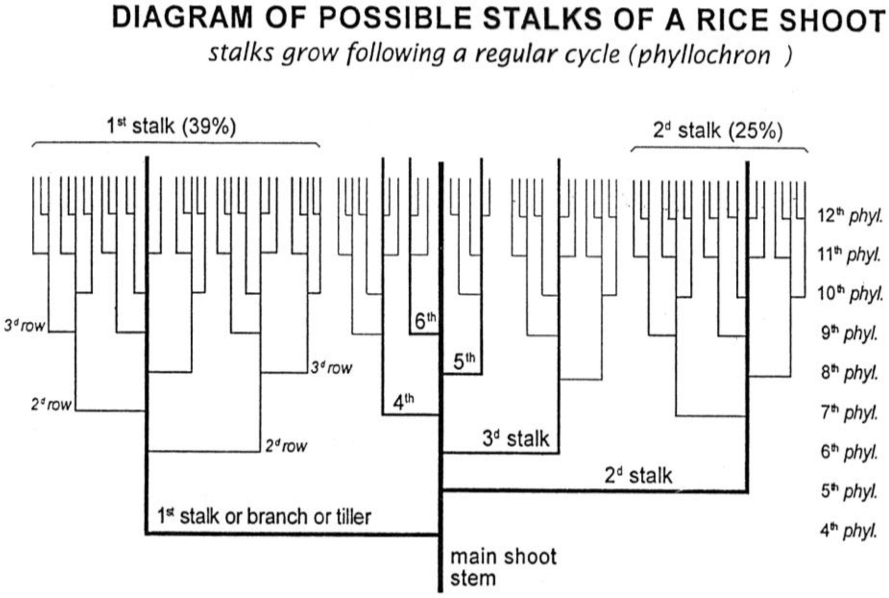
***Note*:**

[15]. *Planting at regular intervals in straight and cross-hatched rows is made easier by using a simple, specially built rake that allows farmers to draw lines in the mud at right angles to create a square pattern (grid) on their field; or by using a simple roller-marker, like a rolling pin used for rolling out bread dough. The transplanted seedlings are set into the intersections of perpendicular lines. In Sri Lanka, women in their second year of SRI transplanting declared this method, involving many fewer plants, easier (and with less back pain) than regular transplanting. That their methods involved no trauma for the plants could be seen when seedlings planted one day with two leaves had a third leaf sprouting by the end of the next day (field visit to farm of H. M. Premaratna, Mallawalana, March 26, 2001).*

[16.] *A whole issue of Crop Science (Vol. 35, No. 1) was devoted to phyllochrons in 1995, but the only contribution on phyllochrons in rice was contributed by Japanese researchers (Nemoto et al. 1995); the rest were mostly on wheat. The 1998 edition of the Oxford University Press Dictionary of Plant Sciences contained unfortunately no entry on phyllochrons in its 600+ pages (Allaby 1998). Even the Japanese encyclopedia on rice science (Matsuo et al. 1997) contains only four pages of descriptive information on phyllochrons, with no consideration of their implications for production. A web search on phyllochrons in 2000 revealed that most available research applied this concept, usefully, only to wheat and to forage grasses.*

[17.] *The main tiller and root emerge from the seed during the 1st phyllochron of growth, 5 to 8 days; then there is no more emergence of tillers or roots during the 2nd and 3rd phyllochrons. This is when it is best to transplant the seedling, i.e., with least set-back to its growth trajectory. Another tiller and root appear in the 4th phyllochron, and also in the 5th. Thereafter, the tillering and associated root growth proceed according to what is known in biology and mathematics as a 'Fibonacci series' -- 1, 1, 2, 3, 5, 8, 13, 20, 31, etc., where the new growth in each period is equal to the sum of the growth in the two preceding periods. Beyond the 10th phyllochron, there appear to be physical space constraints on tiller and root emergence for rice plants which make the Fibonacci series from this point on more approximate rather exact.*

A schematic representation of tillering patterns, organized in terms of phyllochrons, as worked out by Fr. Laulanié from the analysis of Katayama, is shown in fig.- 4 below.



With conventional rice-growing practices, close spacing and hypoxic soil conditions plus transplanting more mature seedlings combine to *slow down the biological clock,* so plants cannot achieve their maximum tillering potential. SRI plants with over 100 panicles have continued their vegetative growth into a 13th phyllochron, and the plant shown in Fig. 1 had extended its vegetative growth into the 15th phyllochron.

Rice seedlings that are transplanted after the beginning of the 4th phyllochron, and certainly ones transplanted much later than this, will not achieve their full yield potential. This physiological effect will be compounded if seedlings have been traumatized during transplanting and if hypoxic soil then induces root degeneration. Root growth, tillering and grain filling will all be reduced under these suboptimal growth conditions. Optimal conditions enable the plant to complete a larger number of phyllochrons before panicle initiation, important because under favorable conditions, with root systems intact, this is an accelerating process.

- **Phenotypical observation: nutrient uptake is best understood as demand-driven**

Another line of plant research that challenges the concept of "maximum biological yield" within the range now proposed concerns the current provision of chemical nutrients in inorganic form to force the pace of plant growth. SRI experience shows that accelerating plant growth through changes in management practices is more effective for getting better crop performance than increasing the soil nutrient supply.

The common view was cited above that N is the main constraint on higher yields, and that applying chemical fertilizer will give higher yields -- even while scientists report that yields "peak" at around 8 t ha^{-1}, even with application of 200 kg ha^{-1} of N fertilizer. Applying more synthetic N in the plant root zone at some point starts *lowering* rather than raising yield.[18]

The most far-ranging discussion we have found on nutrient uptake by rice plants is by Kirk and Bouldin (1991), who entitled their examination of issues as 'speculations.' Their thoughts, based on a summarization of what is known empirically, are prescient and supportive of what has been seen with SRI. A central point they make is that *the uptake of nitrogen by rice roots is independent of the concentration of N at the roots' surface* (1991: 199). When plants' internal N status is satisfactory, their roots down-regulate and reduce their uptake of N, even exuding N into the rhizosphere when the plants have no need for it. More detail on plant roots' 'down-regulation' to give off N is provided in Ladha *et al.* (1998: 46-49).

***Note*:**
18. *"The use of fertilizer-N has increased with time, but the yields have often remained constant in both experimental and farmers' fields…There is no significant increase in yield beyond 150 kg ha^{-1} [of added N], although N uptake increased beyond those levels in many lines" (Ladha et al., 1998: 41, 59).*

This analysis recalls the adage that "you can lead a horse to water, but you cannot make it drink." One can give rice plants a greater supply of N in the soil, but unless they need it, they will not utilize it, and indeed it may even be harmful. This helps to explain the low observed nitrogen-use efficiency with most applications of N fertilizer on irrigated rice crops, noted above.

The standard conditions for growing irrigated rice fairly dense planting and flooded soil – serve to lengthen phyllochrons and thus to slow plant growth. It should not be surprising that when rice plants are not tillering rapidly, and are not extending their root system actively downward, they will have less demand for N than do plants that -- as with SRI practices embark on a rapid sprint of accelerating growth beyond the 8th phyllochron. A plant that is on a growth trajectory to have 84 tillers by the time of panicle initiation has a very different demand for N than one that will produce only 5, 10 or maybe 15 tillers.

Although we now know that rice plants can not be forced to take up more N than they need, much agronomic and plant breeding research has been premised on a 'supply-side' approach to plant nutrition. We can compare this to the *pate de foie gras* strategy of force-feeding geese to make them grow larger, fatter livers -- to be able to produce more *pate* for French palates. Accelerated growth has been sought by providing inorganic nutrients rather than by creating optimal growing conditions that will accelerate growth processes and thus create greater *demand* for N and other nutrients.[19]

There are multiple reasons to conclude that current thinking about "maximum biological ceiling" is poorly founded, based on folk-wisdom assumptions about rice being an aquatic plant and on mechanistic concepts of plants' functioning, ignoring the critical importance of roots and the many intricate interdependencies between roots and above-ground plant organs. There is, surely, such a thing as a ceiling, but there is little reason to believe, based on the literature or on experience from SRI practice, that it has yet been approached for rice.

There are, however, still some important unresolved issues of plant nutrition with SRI that need to be addressed. Plants certainly need nutrients, and of course adequate N for vegetative growth and for grain formation. Simply creating a demand for nutrients does not ensure that there will be an adequate supply. As discussed in the next section, SRI experience in Madagascar where much higher yields have been attained from soils that when assessed in standard chemical analyses are considered to be extremely poor. SRI experience thus raises questions about how we can better understand plant nutrition and plant-soil relationships. Biological processes, particularly microbial factors, surely deserve more investigation to expand upon current thinking that has focused on nutrition primarily in inorganic chemical terms.

Assessing and improving soil fertility by considering biological processes

The yields being reached in Madagascar are not easily explainable according to present ideas about plant nutrition since the soils there are generally so poor. Specifically, soils in the area around Ranomafana from where SRI work commenced are very deficient according to accepted soil chemistry measurements and criteria.

***Note*:**

19. *Another problem with this supply-side approach is noted by Ladha et al. (1998: 43): "excessive uptake of fertilizer-N leads to increased risk of disease and to lodging." Although this is widely recognized, Ladha and his associates write about how to modify the rice plant genetically so that it can take up more N. Farmers in many countries who have tried SRI methods have reported, without prompting, that they observe fewer pest and disease problems with SRI practices and rarely have lodging, despite the heavier panicles.*

A study done by the National IPM Program in Vietnam in 2006-06 in 8 provinces, evaluating the prevalence of two major diseases (sheath blight and leaf blight) and two major pests (small leaf folder and brown planthopper), found 55% less naturally-occurring damage or infestation in the spring season and 70% less in the summer season in farmers' SRI plots compared to adjacent plots managed with conventional rice cultivation methods (IPM 2007).

Research in China (Zhao et al., 2009) has found that with SRI management, the highest yields were obtained with lower rather than higher applications of inorganic N fertilizer. In 2005 trials, highest SRI yield (7.28 t ha^{-1}) was obtained with 80 kg N ha^{-1}, while the highest yield with conventional practices (6.42 t ha^{-1}) was with 240 kg N ha^{-1}. In 2006, the highest SRI yield (6.88 t ha^{-1}) was again with only 80 kg N ha^{-1}, while highest conventional yield (6.07 t ha^{-1}) was with 180 kg N ha^{-1}. That SRI yields were consistently higher than traditional flooded (TF) cultivation with lower rates of N fertilization indicates that with more organic inputs to the soil under SRI management,, more of the N taken up for higher yield is from biological sources. "With both SRI and TF, the highest N application was associated with decreases in grain yield, N use efficiency and water use efficiency" (Zhao et al., 2009, emphasis added). Very similar results are reported from similar trials in Odisha state of India by Thakur et al. (2013).

A soil science PhD thesis for North Carolina State University concluded [ ] based on 20 random deep soil samplings that [ ] given the parent rock from which the soils were formed:

> there are no significant areas of naturally fertile soils within tens of kilometers of the park boundary. The pH values in water range from 3.9 and 5.0, with most values between 4.2 and 4.6….The levels of exchangeable bases (Ca, Mg and K) are low to extremely low in all horizons. The subsoil horizons contain virtually no exchangeable bases. [Available] Phosphorus levels for all horizons are below 3.5 parts per million (ppm), far below the 10 ppm level, which is generally considered to be the threshold at which large crop-yield reductions begin to occur (Johnson, 1994: 6-7).

Further, the two main soil fertility constraints, low nutrient levels and soil acidity, are ones that:

> cannot be realistically managed by low-input technologies such as composting or even manuring. The nutrient-poor soils give rise to nutrient-poor plant residues and manure… The only viable strategies for producing sufficient agricultural yields are to use man-made fertilizers or to continue slash-and-burn practices (Johnson, 1994: 7).

Before SRI was introduced to farmers around Ranomafana in 1994, agricultural advisors from NC State had worked with a few farmers there to test raising rice yields through use of fertilizer and new high-yielding varieties. These techniques achieved average yields of 3 t ha^{-1}, compared to the local average of 2 t ha^{-1}, and reached a maximum of 5 t ha^{-1} (Del Castillo and Peter 1994). Yet on these same soils[] that had been judged to be thoroughly deficient by standard soil science criteria, farmers using SRI methods – and not depending on chemical fertilizer -- averaged over 8 t ha^{-1}, with the best farmer reaching 16 t ha^{-1}. How to explain a four-fold increase?

Current models of soil-plant nutrition can be characterized as 'banking models,' where there is assumed to be some initial deposit of nutrients in the soil, and then subsequent balances depend on how many nutrients have been added back to compensate for how many nutrients have been taken out by the crop, or lost through erosion and other processes such as N volatilization.[20]

Since farmers following SRI ideas are putting on their fields only compost made from plants grown in this nutrient-deficient soil, and occasionally some manure or a little fertilizer, one should expect yields to decline rapidly. But farmers report that usually their yields increase over time, as they gain greater skill and confidence in the methods. It is possible that skill effects masked some nutrient loss; but this does not appear to be the case as farmers usually reported that with SRI their soil quality improved. Quite possibly this is because with larger canopy and root systems, more sugars, amino acids and vitamins are injected into the soil as root exudates, thereby enriching the rhizosphere and supporting greater abundance and diversity of microbial life there.

There are inconsistencies in the literature concerning rice plant nutrition that should have caused some doubt about the prevailing concepts framing this subject. The loss of N due to volatilization and leaching is regarded as a particularly serious problem when chemical fertilizers are added to the soil. Yet based on an analysis of trials with 180 varieties of rice in uniform soil, assessing how N fertilizer applications affect grain yield, Ladha *et al.* (1998) reported that for most varieties, maximum yield was achieved with 150-200 kg of N ha^{-1}. However, when disaggregating the trials they found that medium-term varieties (119 days ± 4) produced their highest yield with 150 kg N ha^{-1}, while longer-term varieties (130 days ± 4) attained their maximum yield with one-third less N, just 100 kg ha^{-1} (pp. 58-59).

***Note*:**
[20.] *Discussing the 'banking model' critically does not mean that there are or can be no absolute limits on soil nutrient supply. It calls attention to the way that focusing on 'available' nutrient supplies produces estimates of inorganic nutrients such as N, P, K, Mn and Cu, as if these are the total supply to be considered. In fact, biological processes can access nutrients in forms unavailable to plant roots and can transform these into forms that can be accessed, through processes such as P solubilization (Turner and Haygarth 2001). As discussed below, microbial populations themselves constitute a potentially large source of available nutrients in organic form, affected by soil, plant, water and nutrient management practices. The "bank" is thus larger than usually described by soil analyses that assess mostly inorganic forms of N, P and K and not much else*.

If N is as crucial a determinant of yield as most rice scientists believe and if volatilization and leaching cause significant losses of N, why should *longer*-duration varieties perform best when given only about *half* as much N fertilizer per hectare as the researchers concluded was best for most varieties, and specifically only two-thirds as much as maximized yield for medium-term varieties? This analysis gives additional reasons to question the 'yield ceiling' concept.

Research by Kronzucker *et al.* (1999) has shown that a given amount of N produces *40 to 70% more yield* when the N was provided equally in the form of ammonium (NH_4^+) and nitrate (NO_3^-), rather than being provided only as ammonium (p.1041). This surprised the researchers since ammonium ought to be 'preferred' by rice plants as a source of N because metabolizing NH_4^+ requires less energy than for utilizing nitrate. They found further that a combination of NH_4^+ and NO_3^- led to better yields than providing N in either form (NH_4^+ or NO_3^-) by itself. This relates directly to the SRI practice of not growing rice under flooded (anaerobic) conditions, where practically all of available N will be in NH_4^+ form. Providing water to paddies in daily small amounts, with intermittent drying of the soil until surface cracks appear, or alternately wetting and drying the paddies will ensure that the N is available in some combination of the two N forms, directly contributing to yield enhancement. What Kronzucker *et al.* did not underscore is that the forms of N are converted in large part by microbial activity.

From their analysis, Ladha and associates suggested that N from *organic* rather than inorganic sources is probably more critical for rice plant performance. As noted above, just because faster-growing rice plants will have demand for more N does not mean that they will have an adequate supply; demand does not necessarily create its own supply, although maybe in the symbiotic underground realm this is possible. [paragraph break]

The yields with SRI practices when used as recommended are beyond what can be accounted for by available N supplies measured in the soil. This directs some of our attention to biological nitrogen fixation (BNF). Although most people, and even many scientists, still associate BNF with leguminous species, practically all of the gramineae species including rice benefit from BNF that is provided by soil microbes living in, on and around the roots (Döbereiner 1987; Boddy *et al.*, 1995; Baldini *et al.*, 1997).[21]

When BNF has been studied for lowland rice, some but not very great benefits from this process have been found (Roger and Ladha 1992). But these evaluations have been done within a paradigm that considers rice to be an aquatic plant that performs best under continuous flooding. Maintaining the soil in hypoxic condition eliminates the contributions that aerobic microbes can make to BNF. While some microbes that can fix nitrogen are anaerobic, most are aerobes. [P] Döbereiner found that for sugar cane, when the soil had been previously fertilized with inorganic N and when the cultivars used had been fertilized in previous generations, processes of BNF were diminished and even suppressed. This is attributable to the effect that inorganic N has in suppressing the production of nitrogenase, the enzyme necessary for BNF, by bacteria and plants (Van Berkum and Sloger, 1983).

Certainly it would be premature to propose that the N needs of the rice plant can be met by BNF alone. But results with SRI suggest that there can be very significant BNF in soils that have low inorganic N status, provided that they have a good supply of soil organic matter (C). How else to account for a quadrupling of yield, from 'poor' soils, just by making soil amendments of organic matter?

The value of compost goes well beyond the kinds and amounts of nutrients that the organic matter itself contains; this considers compost in purely chemical terms. There is no disagreement that adding organic matter to the soil improves its structure and functioning with better aggregation and porosity. It probably contributes also by 'priming the biological pump' of processes mediated by microorganisms which are symbiotically associated with plant roots and the root-soil interface. [22]

***Note*:**

[21]. *It has been seen, for example, that rice plants benefit from BNF from endophytic bacteria that grow on leaves (Kannaiyan et al., 1999)*

[22]. *Research undertaken at Michigan State University's Kellogg Biological Center, not yet published, indicates that most soil microbes have the genetic potential to engage in BNF, even if they do not normally do so (Frank B. Dazzo, personal communication).*

The importance of these processes has apparently been underestimated in crop science because of disciplinary divisions, where plant physiology, microbiology, soil chemistry, soil fertility, and biochemistry all get studied separately. Most plants release some portion of the photosynthate that they generate through photosynthesis into their root zone in the form of exudates. As much as 30% of the C fixed via photosynthesis may end up as root exudates. Sugars, amino acids and even vitamins are shared with microorganisms in the rhizosphere through exudation.[23]

Many plants provide some of their energy supply to nourish the mycorrhizal fungi that are integrated into their root systems to enhance nutrient uptake. Such symbiotic relationships have evolved over about 400 million years, creating plant dependency on microbes' contribution to their nutrition. Plants must be gaining more value from these processes than the value that they could get from retaining these nutrients for themselves and not exuding them into the soil. Microbial populations in turn expand (or contract) according to the nutrient supply that the roots provide, together with the amounts of organic matter in the soil and of chemicals in mineral (inorganic) form.

Greater soil aeration, as achieved with SRI methods, is beneficial at least for those microbes that are aerobic, which include the generally-neglected mycorrhizal fungi. Because irrigated rice soils are hypoxic, and fungi cannot survive under anaerobic conditions, the potential benefits of mycorrhizae (fungal-root complexes) have been forgone by plants growing in flooded rice paddies for thousands of years.

Mycorrhizal fungi absorb not just N, P and K from the soil but also Ca, S, Fe, Mn, Cu and Zn and translocate these nutrients to the plants in whose roots the fungi have established themselves symbiotically (Habte and Osorio, 2002). The hyphal filaments of mycorrhizal fungi can extend from the root surface as much as 10-12 cm into the soil, enabling root systems enhanced by mycorrhizae to explore as much as 100 times more volume of soil than could be accessed by the roots alone (Sieverding, 1991).

Since mycorrhizal hyphae have a smaller diameter than plant roots, they can reach into spaces and places in the soil that are inaccessible to roots, thereby enhancing the variety as well as the quantity of nutrients available to the plant. In addition, mycorrhizae can stimulate hormone production in plants, aid in improving soil structure, suppress plant diseases including nematode infection, enhance leaf chlorophyll levels, and enable plants to tolerate various kinds of stress (see review article by Habte and Osorio, 2002). Part of the SRI effect could be due to the facilitation of mycorrhizal growth and functioning in rice soils that are not kept continuously inundated.

One of the nutritional services that aerobic microbes provide to plants is solubilization of P. When P is measured in the soil, usually just inorganic P is assessed, referred to as 'available phosphorus,' but little weight is given to the adjective, as the measurement is considered to refer to total P. The soils around Ranomafana, as reported above, were found to have available P concentrations of only 3-4 parts per million. This is less than half the amount that is usually considered as a threshold for having yield declines (10 ppm).

Also, in addition to making P available through solubilization, microbes can acquire P for their own growth from reserves in the soil that are unavailable to plants directly. When these microbes expire, their nutrient contents become available to plant roots. Because of these processes, the amount of P in soil is not a fixed amount but something that varies according to kinds and levels of microbial activity. The reserves of 'unavailable P' that can be accessed through biological activity are 20-40 times more than the usual amounts of 'available P' that are registered in soil testing. Total P is the sum of phosphorus in available and unavailable forms.

***Note*:**

[23] *This is an area of relatively little research, given its potential importance, but also an area that presents many analytical and measurement difficulties because of the (small) scale of the processes involved and their complexity. The amount of carbon released from roots growing in soil amounts to about 20% of the total plant dry matter, according to Rovira (1979). Johnen and Sauerbeck (1971) found that the amount of C exuded into the rhizosphere is up to 3 times the amount of C present in the root at harvest. Martin (1977) reported that about 40% of the C that is translocated to the roots is released into the soil. Much of this total is from the breakdown of root cell walls rather than through exudation. The rhizosphere is that area around the plant root system that is influenced by processes of the root. My colleague formerly at Cornell and now with the World Bank, Erick Fernandes likens it to a very thin rubber glove fitting over the root system, with millions of fingers. On this, see Römheld and Neumann (2006).*

The water management methods recommended with SRI include alternately wetting and drying the soil. Recent research has indicated that this process itself increases the amount of organic P available in soils as microbes release their cell contents when bursting under osmotic shock. The increases in available P measured by Turner and Haygarth (2001) after rewetting and drying ranged from 185 to 1,900%! Their analysis suggests that this process may also increase the supplies of other soil nutrients in organic form. This effect has been known for decades, but it has not been examined very thoroughly because of the preoccupation with inorganic sources for plant nutrition. The volume of microorganisms in the soil is huge, as many as 15 tons per hectare of bacteria, fungi, actinomycetes, etc. (Brady and Weil, 2002).

CONCLUSIONS

As suggested at the beginning of this article, SRI still raises more questions than we have answers for. We are already seeing, however, that it can make a substantial contribution to increasing the world's supply of rice. With SRI management, large yield improvements have been seen in agro-ecosystems as different as the northern mountain regions of Afghanistan (Vincent and Ramzi 2011) and the Timbuktu region of Mali on the edge of the Sahara Desert (Styger *et al.*, 2011). In both places where average yields of irrigated rice have been 4.5-5.5 tons ha^{-1}, average yields of 8-10 t ha^{-1} have been achieved in farmers' fields, without dependence on purchased inputs. Moreover, with appropriate adaptations, similar improvements have been seen with rainfed rice production, and then with other crops like wheat, sugarcane, tef, and millet.

This is not to suggest that we should be doubling rice yields around the world. There is no need for growing twice as much rice, even if this would be possible with SRI methods, if only because of the deflation that this would cause for rice prices. Rather we anticipate that the factor productivity increases possible with SRI will permit redeployment of some or much of the land, labor and water that are currently required for rice production for other agricultural uses that are more productive and profitable than simply growing more staple food.

The SRI experience to date suggests substantial opportunities for increasing agricultural sustainability by refocusing attention on combinations of plant, soil, water and nutrient management practices, evaluated particularly in terms of their impact on soil microbiology as an intermediary dimension of agricultural production processes. Some recent research findings suggest that there can be a very positive effect from symbiotic endophytes originating in the soil but living in, on and around the leaves (Uphoff *et al.*, 2013). The phyllosphere is much less known and studied than the rhizosphere, about which we still know much too little. We hope that SRI will open some new lines of inquiry in the agricultural sciences that can contribute to other advances in understanding and practice, particularly paying more attention to plant roots and their functioning.

Present knowledge about plant growth and nutrition has led to many advances in agricultural production, but this does not mean that it is complete or perfect. Current thinking about 'maximum biological yield' and 'yield ceilings' as a function of genetic characteristics appears to hinder more than help us increase our knowledge about rice. In particular, more attention to microbial contributions and roles in plant nutrition is likely to yield more benefit than further studies of plant nutrition that are framed more in chemical, rather than in biological, terms.

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