CHAPTER FOUR

Scientific Underpinnings of the System of Rice Intensification (SRI): What Is Known So Far?

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Contents

Abstract

During the last 10 plus years, the system of rice intensification (SRI), a methodology for rice cultivation with many reported benefits, has been promoted in a number of countries, particularly in the major rice-growing nations of China, India, Indonesia, Vietnam, and Cambodia, which produce two-thirds of the world's rice. However, reports of substantial yield increases and phenotypic changes resulting from SRI management have been challenged on various grounds in the scientific literature.

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The debate has been among the most contentious in recent agronomic forums, although it has been receding in recent years as evidence continues to accumulate. This paper reviews information now available in the scientific literature that supports the multiple agronomic, plant physiologic, and soil microbiologic foundations for the reported SRI performance, and discusses how these effects are becoming even more relevant in the context of changing climates.

1. INTRODUCTION

Rice (*Oryza sativa* L.) is the foremost staple food in Asia, providing 35–60% of the dietary calories consumed by more than 3 billion people (Fageria, 2007). The crop is grown under a wide range of agroecological and water management conditions, varying from fully controlled irrigation to rainfed conditions, in both uplands and lowlands.

The Green Revolution, which started some 50 years ago and aimed at raising the yields of rice and other major cereal crops, was based largely on the breeding of semidwarf cultivars that are responsive to water and mineral fertilizer inputs (Swaminathan, 2007). As rice yield increases in many Asian countries have reached a plateau in recent years, it is becoming questionable whether that research strategy can provide significant further yield increases (Cassman, 1999).

This deceleration in rice productivity growth is partly associated with declines in soil fertility, salinization, land degradation, erratic rainfall, and extreme weather events (Nelson et al., 2009). But it is also noteworthy that yields in rice breeders' trials at the International Rice Research Institute (IRRI) have not significantly increased over the past 30 years (Sheehy et al., 2007). The gene-dependent, input-intensive strategy for raising rice yields thus appears to have encountered what economists call diminishing returns.

Population growth, declining arable land per capita, and water scarcity, as well as problems of the quality and reliability of water for agriculture, present multiple challenges for achieving food security now and in the years ahead (Fedoroff et al., 2010). The constraints and hazards of climate change are adding to these challenges (Wheeler and Braun, 2013). It is expected that food production will need to rise by 60% between now and 2050 to satisfy the demand of a population expected to reach or surpass 10 billion people (FAO, 2012).

In Asia, human population is expected to rise from 3.9 billion to 5.3 billion, a 36% increase over the next 50 years (UNFPA, 2005) and demand for rice will grow faster than for any other crop because population growth will be greatest, absolutely if not relatively, in the rice-consuming and rice-producing regions of the world (Dawe, 2007). At present, each hectare of land used for rice production in Asia provides food for 27 people; but by 2050 each hectare will have to support at least 43 people.

Agriculture is the sector most sensitive to water scarcity; it is both a cause and a victim of water scarcity. It is likely that if today's food production systems and environmental trends continue, this will lead to water crises in many parts of the world, so "business as usual" is not an option. Real changes are needed in the way in which water is allocated and used if future crises are to be averted (FAO, 2012).

It has been estimated that for every 1°C rise in mean temperature, there will be a corresponding 7–10% decline in average rice yields (IWMI, 2007). The International Food Policy Research Institute has predicted a 12–14% decline in world rice production by 2050, mainly due to changing climate scenarios, despite the greater need for this staple cereal (Nelson et al., 2009). We will thus need to produce more food to feed our growing populations, sustainably as well as in socially and environmentally acceptable ways, from less land and with reduced water resources (Schneider et al., 2011; Swaminathan, 2007).

In these respects, the system of rice intensification, widely known as SRI, might offer multiple advantages. Although its origin has been largely empirical, its scientific foundations have been strengthened over recent years as will be elaborated in the following sections. SRI is a rice crop management system developed in the 1980s in Madagascar (Laulanié, 1993). It is based on a set of interdependent agronomic practices (Table 1) that together, and often respectively, can lead to increased yields with reduced levels of production inputs. The methodology was initially tested for about 10 years and on a limited scale in Madagascar; more serious promotion outside that country only started some 10–15 years ago. Presently, the use of SRI methods is spreading in most Asian countries, and more recently in some two dozen countries in Africa and Latin America.

According to Kassam et al. (2011), SRI methods by modifying crop, soil, water, and nutrient management practices can raise substantially the productivity of land, water, seeds, and capital (and often, even of labor) used in irrigated rice production. Similar improvements have been reported also for rainfed rice, and for a wide range of other crops including wheat, sugar cane, millet, mustard, legumes, etc. (Abraham et al., 2014; Behera et al., 2013). However, these reports are still not universally accepted.

Table 1 SRI practices and their effects.

Practices	Effects	References
Transplanting of young seedlings	● No or reduced transplanting shock ● Early and increased tillering and root growth ● Earlier transplanting date into the main field extends the time for rooting and tillering	Menete et al. (2008), Mishra and Salokhe (2008), Pasuquin et al. (2008)
Single seedling per hill transplanted at shallow depth	● Seed requirements are greatly reduced ● Reduced competition for nutrients, water, radiation, and space within a hill ● Open canopy structure gives greater light interception by leaves and less shading of lower leaves, enhancing the supply of photosynthate, especially to the roots ● Early root growth enhanced, leading to increased cytokinin flux toward the shoots, delayed senescence of leaves and roots, and increased photosynthesis	San-oh et al. (2004, 2006), Thakur et al. (2010b)
Wider spacing	● More space (below- and aboveground) for roots and shoots to access nutrients, water, and light ● Promotes more profuse growth of roots and tillers	Thakur et al. (2010a, 2013)
Moist and nonflooded water management regime	● Aerobic (nonhypoxic) conditions of the soil favor root health and functioning, and also support more abundant and diverse communities of beneficial aerobic soil organisms ● No degeneration of roots, which under flooded soil conditions become degraded by as much as 75% by the phase of flowering	Jagannath et al. (2013), Jain et al. (2013), Satyanarayana et al. (2007), Suryavanshi et al. (2013), Thakur et al. (2011), Yang et al. (2004, 2012), Yang and Zhang (2010), Zhao et al. (2009)

	• Water savings up to 40% • Energy savings for pumped water • Reduced GHG emissions	
Intercultivation to control weeds	• Churning up and aerating the surface soil • Activates beneficial microbial, physical, and chemical soil dynamics • Weed biomass is incorporated into soil as green manure • Weeding costs can be reduced	Satyanarayana et al. (2007), Xu et al. (2013)
Increased use of organic manures	• Improves soil structure and porosity • Promotes root growth and root activity • Sustained nutrient supply over longer period • Favors growth and activity of soil biota	Gopalakrishnan et al. (2014b), Thies and Grossman (2006), Yang et al. (2004)

2. THE SRI CONTROVERSY

SRI has been a subject of controversy among many scientists stemming from some very high reported yields that were achieved in soils with low inherent fertility, and this is in spite of greatly reduced rates of irrigation and without relying on external inputs (Stoop et al., 2002; Uphoff, 1999, 2003). In response, some rice researchers have argued that the success stories on SRI are only anecdotal and not supported by scientific evidence or are biologically unattainable (Dobermann, 2004, 2013; McDonald et al., 2006, 2008).

Reports of yield benefits and phenotypic changes with SRI management have been challenged on various grounds (Dobermann, 2004; Sheehy et al., 2004; Sinclair, 2004; Sinclair and Cassman, 2004; McDonald et al., 2006). This skepticism of SRI has been responded to with empirical evidence in respectable journals, for example, Stoop and Kassam (2005), Thakur (2010), Uphoff and Randriamiharisoa (2002), and Uphoff et al. (2008); but so far this has not resulted in a wider and more general acceptance of SRI's claims and methods by the international agricultural research establishment (e.g., Fischer et al., 2014).

The controversy has in any case stimulated considerable experimentation and field testing, which has led to a growing body of scientific literature published over the past dozen years (http://sri.ciifad.cornell.edu/research/JournalArticles.html). Meanwhile, the use of SRI methods has continued to spread. The SRI-Rice Center at Cornell University has reports from over 50 countries where these methods have given more productive phenotypes from given genotypes (http://sri.ciifad.cornell.edu/countries/index.html). In five countries, which produce two-thirds of the world's rice (China, India, Indonesia, Vietnam, and Cambodia), governments are supporting the spread of SRI knowledge and practices based on their own evaluations and farmer experience.

Presently, the number of farmers in these countries using some or all of the recommended SRI practices (listed in Table 1) is estimated to approach 10 million, on about 3.5 million hectares. This number of farmers is already more than half as many as are using genetically modified crops (James, 2013), although the SRI area is a fraction of the GM area since it is being practiced mainly by smallholders. The resources behind the extension of SRI have been only a tiny fraction of the commercial and governmental resources promoting GM technology. It is timely to review the currently available information and to assess the scientific basis for SRI, complementing some earlier analyses (Horie et al., 2005; Mishra et al., 2006; Stoop, 2011;

Toriyama and Ando, 2011), besides assessing SRI's possible significance for countering the adverse effects of a changing climate.

3. SRI PRACTICES AND THEIR REPORTED EFFECTS

The SRI methodology diverges in fundamental ways from what has been standard agronomic management for irrigated rice as described in De Datta (1981). SRI involves particularly the practices of (1) transplanting young seedlings, preferably 8–12 days old (at 2–3 leaf stage), quickly, carefully, and at shallow depth (1–2 cm deep); (2) transplanting single seedlings in a square pattern with wide spacing, usually about 25 × 25 cm but wider or closer according to soil conditions and variety; (3) maintaining mostly aerobic soil conditions rather than continuous flooding during the vegetative growth period; (4) adding organic manures like compost or mulch to enhance soil organic matter; and (5) controlling weeds with a mechanical hand weeder that actively aerates the soil (Stoop et al., 2002).

SRI should not be considered a technology, nor as a fixed recipe, but rather as a set of interdependent agronomic practices that modify current plant, soil, water, and nutrient management (Uphoff, 2003). There are important interactions between some of the practices, for example, interaction between plant density and the soil moisture regime poses considerable problems in properly assessing SRI (Stoop et al., 2009). This means that studies looking in detail into individual SRI practices, for example, seedling age, irrigation and fertilization regimes, etc., one at a time and in isolation from other practices, are likely to produce questionable, if not biased, data and conclusions.

Table 1 presents the respective practices that constitute the SRI management strategy. These have proved to be advantageous for irrigated rice production and, with certain modifications, also for several other rainfed crops (Abraham et al., 2014). The beneficial effects of these various practices are largely based on positive feedback mechanisms between roots and shoots, which have also been documented in studies that were not connected to SRI, notably:

- Transplanting *young seedlings* is advantageous for early crop establishment, in part because this avoids or minimizes "transplanting shock," thereby enhancing the growing plants' tillering and rooting (Pasuquin et al., 2008).
- *Single seedlings* per hill have been found to be superior to transplanting three seedlings per hill (as recommended for conventional approaches),

improving tillering, root development, RuBisCO contents, and cytokinin levels (San-oh et al., 2006).

- *Widespacing* reduces interplant competition for nutrients, water, light, and air, which significantly enhances individual hill performance under SRI management. This permits prolific tillering and associated root development, along with increased grain development that can more than compensate for reduced plant populations on an area basis (Thakur et al., 2010a, 2014).
- *Alternate wetting and drying* (AWD) is considered an effective water-saving technology in rice production with studies showing that moderate AWD not only saves water, but also can increase grain yield (Zhang et al., 2009a).
- *Organic manure application* under AWD has been seen to increase significantly the uptake of N, P, and K, causing a significant increase in filled grains per panicle, 1000-grain weight, and grain yield (Yang et al., 2004). The beneficial effect of an integrated (organic and mineral) fertilizer strategy has been significant for grain yields also under waterlogged conditions (Yang et al., 2004).
- *Intercultivation/weeding* is essential for SRI because under an AWD moisture regime, weed growth readily becomes problematic. Mechanical weed control has the advantage of aerating the soil while incorporating the weeds into the soil, which enhances both root growth and health and soil populations of beneficial soil microbes (Anas et al., 2011).

These respective individual practices, because of the interactions involved, for example, between soil moisture/irrigation regime and plant spacing/density, are most effective when used in combination with other SRI practices (Uphoff and Randriamiharisoa, 2002).

SRI practices have been studied and reported in many countries: Madagascar (Barrett et al., 2004; Uphoff, 1999), Bangladesh (Husain et al., 2004; Latif et al., 2009), China (Wang et al., 2002; Yuan, 2002; Zhao et al., 2009), Gambia (Ceesay et al., 2006), India (Satyanarayana et al., 2007; Senthilkumar et al., 2008; Sinha and Talati, 2007, Thakur et al., 2010b, 2011, 2013), Indonesia (Sato and Uphoff, 2007), Iraq (Hameed et al., 2011), Myanmar (Kabir and Uphoff, 2007), Nepal (Dahal and Khadka, 2012), Panama (Turmel et al., 2011), Sri Lanka (Namara et al., 2008), and Thailand (Mishra and Salokhe, 2010).

Most of these studies have identified and assessed the impact of SRI methods on rice plants' phenotypic expression such as increases in tiller number, panicle length, grain number and size, etc. Only a few studies have looked into the physiologic changes that can be induced in the same genotype by altering the plants' environmental conditions for growth. The following sections review some of the morphologic and physiologic changes in phenotypes that have resulted from SRI type management and that together provide scientific explanations for the SRI phenomenon.

4. SCIENTIFIC FOUNDATIONS OF THE RECORDED SRI FEATURES

It is increasingly evident that two basic mechanisms are largely responsible for SRI effects, resulting directly from the SRI management practices listed in Table 1. These two factors are, however, belowground, and therefore, they have received little attention from farmers and most researchers. To properly understand the main effects of SRI management, it should be recognized that these are largely caused by:

1. *Profuse root systems* that support the plants' canopy, leaf and tiller growth, and grain filling,
2. *Prolific and diverse populations of beneficial soil organisms* (bacteria, fungi, actinomycetes, mycorrhizae) and the food web that builds upon them.

This soil food web extends upward to the mesoflora and mesofauna, which are prolific although still mostly invisible, and finally to the earthworms, mites, and many other visible organisms that feed upon them. Together, these decompose organic materials, improve the soil's structure, and fix, solubilize, or recycle nutrients (macro- as well as micronutrients) for uptake by plants. The extent, functioning, and diversity of the soil biota regulates the decomposition of organic materials (their major source of nutrition) and elimination of waste products, thereby creating productive potential from what are otherwise lifeless elements (Thies and Grossman, 2006).

4.1 Phenotypic Changes to be Accounted for

SRI practices cause large changes in the morphologic characteristics of rice plants, in their roots, tillering, and canopy, as compared with irrigated rice grown under continuous flooding. These changes have been documented and explained in the past (e.g., Chapagain and Yamaji, 2010; Mishra and Salokhe, 2010; Stoop, 2011; Thakur et al., 2011; Uphoff, 2012) and can be summarized as follows.

4.1.1 Root Growth

SRI practices have generally resulted in vigorous root growth and enhanced root activity (Hameed et al., 2011; Mishra and Salokhe, 2010; Thakur et al., 2010b, 2011). This has been assessed in various ways. First, by assessing root-pulling resistance, where SRI rice plants offered as much as eight times more resistance per plant than was measured for conventionally grown plants (often planted as clumps of three or more plants/hill) (Barison and Uphoff, 2011). Root growth has also been assessed in terms of effective root depth, total root length, and dry weight per hill recorded at the grain-filling stage. Again, SRI rice has proved far superior than a flooded rice crop (Thakur et al., 2011).

Not only was the root growth enhanced with SRI practices but also the proportion of functional roots (white-colored) was increased. Chapagain and Yamaji (2010) report that before the flowering stage, the average proportion of whitish (functional) and black (nonfunctional) roots was 74:26 under SRI management and 46:54 for continuously flooded plots. Earlier, Kar et al. (1974) had established that roots growing in aerobic soil senesce much less and more slowly. Their research showed that by the time of flowering, 78% of the roots of conventionally flooded rice plants had degenerated, whereas there was practically no degeneration of roots for plants grown in well-drained soil. Finally, under AWD irrigation, root length density (RLD) and root weight density (RWD) were increased as compared with continuously flooded rice (Yang et al., 2004). That roots would degenerate under hypoxic conditions can hardly be considered a surprise.

4.1.2 Tiller Production

The tillering ability of rice plants is seen in the number of phyllochrons of growth that they complete before entering their reproductive stage (Nemoto et al., 1995; Stoop et al., 2002). Phyllochrons are periods (cycles) of plant growth in which one or more phytomers (units of tiller, leaf, and root) emerge from the plant's meristematic tissue. This number increases during the plant's vegetative growth and under ideal conditions, it follows a Fibonacci (roughly exponential) sequence (Nemoto et al., 1995; Stoop et al., 2002).

The length of phyllochrons varies from 4 to 10 days, depending on how favorable the conditions for plant growth are above- and belowground. Their length is influenced jointly by a number of factors: soil and ambient temperatures, exposure to sunlight, spacing between plants, soil nutrient availability, soil friability versus compaction, soil moisture versus desiccation, and soil aeration versus hypoxia (Nemoto et al., 1995).

Young seedlings transplanted under SRI management, with minimal transplanting shock, are able to resume their growth quickly; and under favorable field conditions, they can complete a larger number of phyllochrons by the time of flowering. For older seedlings transplanted densely and under hypoxic (flooded) soil conditions, tillering is seen to be much reduced. The more the number of phyllochrons of growth completed before the plant enters its reproductive phase, the larger will be the number of its tillers (and roots). In one of our studies, 28–34 tillers per plant were produced before anthesis with SRI practices, while rice plants under conventional flooded cultivation reached only up to 13 tillers (Thakur et al., 2010b).

Under very favorable growing conditions, the number of tillers produced by a single plant can exceed 100, and under the most favorable conditions, even more than 200, that is, when more than 12 or 13 phyllochrons (cycles of tiller and root emergence) are completed before panicle initiation (Figure 1). This illustrates the significant growth potential in existing rice genomes if this can be fully exploited as under ideal growing conditions. Epigenetic processes are likely to play a role in this as well, but so far have not been studied.

Figure 1 Stump of a rice plant (modern variety Ciherang cv.) having 223 tillers and a correspondingly huge root system, grown with SRI methods from a single seed in East Java, Indonesia.

4.1.3 Interdependencies Between Roots and Leaves

Rice plants grown under conventional methods of flooding and high plant densities are constrained by competition for nutrients, space, and radiation during their later stages of vegetative growth. Under SRI management, on the other hand, individual young transplants continue to benefit from favorable conditions (including wide spacing) throughout their growth cycle, developing many productive tillers and simultaneously an extensive root system (Katayama, 1951). This can be seen from the diminishing crop growth rate (CGR) in flooded rice during the later phases of vegetative development (Figure 2; Thakur et al., 2011).

In these trials, the RMP employed a plant density (i.e., number of plants m^{-2}) that was six times greater than for SRI. Consequently, the growth rate under conventional practice during the first 50–60 days after germination was 34 g m^{-2} day^{-1} as compared with 22 g m^{-2} day^{-1} for SRI. However, at 60–70 days after germination, this relationship is reversed, because of the profuse tillering by SRI plants that is, 52 g m^{-2} day^{-1} for SRI, compared with 20 g for the conventional planting. This latter response was caused mainly by the senescence of older leaves in combination with the premature root degeneration that resulted from flooding and closely spaced plants. This advantage for SRI plants continues throughout the remainder of the crop growth cycle, and is mirrored underground by a prolific growth of root systems.

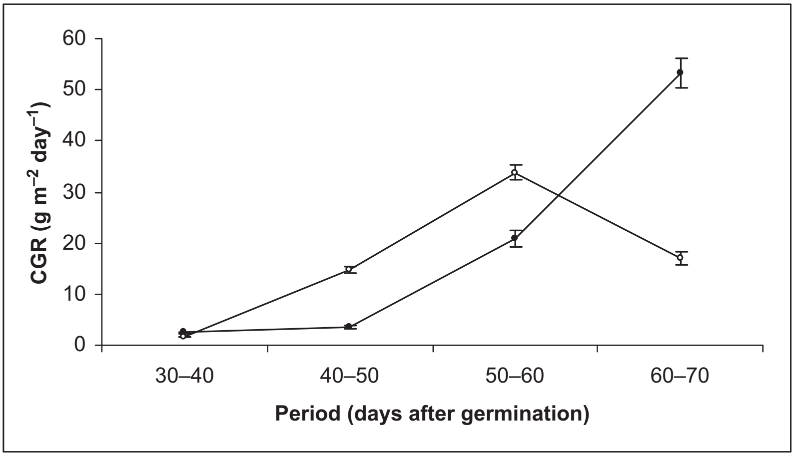

Figure 2 Changes in CGR for rice plants during their vegetative growth stage when grown with SRI or recommended management practices (RMP). Closed and open circles represent SRI and RMP management, respectively. Vertical bars represent SEM ± ($n = 6$). *From Thakur et al. (2011), with permission.*

Apart from an increased number of tillers, the accelerated CGR for SRI plants during their later vegetative growth stage has several other impacts. Notably, the number, size, and thickness of leaves, as well as the plant height and strength of tillers (tiller diameter/perimeter), were all increased significantly. Positive effects on the leaf area index (LAI) and leaf elongation rates, as well as a reduced susceptibility to diseases, were also evident (Thakur et al., 2011). Further, the extensive root systems enhanced the water and nutrient uptake (Thakur et al., 2013). These effects have also been reported earlier by Nguyen et al. (2009) for non-SRI rice plants grown under *saturated* soil conditions as compared with a *flooded* situation. Those research results showed the exploitable potentials of rice seed more generally (provided it is of good quality), which have not been realized under conventional practices of high plant densities and continuous flooding.t

4.1.4 Canopy Structure and Light Interception

Another observable morphologic change in rice plants grown under SRI management is that they have a more open architecture, that is, a greater canopy angle, with their tillers spreading out more widely and covering more ground area at the same time that their more erect leaves avoid mutual shading. Conversely, with conventional management, hill structure is more compact with tillers growing more vertically as induced in closely spaced plantings.

These changes in SRI plants are a response to the shallow transplanting of small/young seedlings and their wider spacing, so that new tillers initially emerge more horizontally from the hills. SRI plants with their more open canopy structure, erect leaves, and higher LAI lead to greater light interception. Trials have showed SRI plants achieving 89% light interception at panicle initiation stage, compared with 78% interception by plants grown under conventional RMP. This 15% advantage was achieved by just 25 SRI plants m^{-2}, six times less than the 150 plants m^{-2} commonly recommended (Thakur et al., 2011). Research unrelated to SRI by Sakamoto et al. (2006) has also highlighted how erect leaves in rice plants can increase both their biomass production and grain yield.

4.2 Physiologic Performance and the Role of Soil Microorganisms

The phenotypic changes discussed earlier profoundly affect not only the physiologic functioning of rice plants under SRI management, but also the scope for interactions between the more extensive root systems and the soil biota. These interdependencies between physiologic processes of belowground roots and aboveground canopy have been widely overlooked in earlier research. It also suggests that research focused exclusively on root genetics (Ahmadi et al., 2014) is unlikely to impact successfully on grain yields and crop resilience. Likewise, the greatly extended root systems of SRI plants, besides favoring the interactions with the soil biota, will also affect the plant's capacity to access nutrients from the soil. These are two major aspects of SRI, both directly affecting crop growth and yield. These issues will be reviewed next.

4.2.1 Physiologic Balance Between Below- and Aboveground Plant Organs

The physiologic aspects of plant–soil–microbe interactions are an extremely complex research domain involving intricate processes at microbial and molecular levels affecting the synthesis of plant hormones and other compounds that are essential to growth as well as to natural plant defense mechanisms against various pathogens (Chi et al., 2010; Gopalakrishnan et al., 2012, 2013). Recently, much progress has been made in these domains that are very relevant in explaining the various SRI features.

Research conducted in Egypt has documented the growth of plant roots being directly affected by soil microorganisms (Yanni et al., 2001). Testing two rice varieties and inoculating them with *Rhizobium leguminosarum* bv. Trifolii E11, researchers found that the presence of certain bacteria in and around the plant roots increased the number of rootlets per plant, the cumulative root length (in cm), the surface area of plants' root systems (in cm^2), and the roots' bio-volume (in cm^3). Chi et al. (2010) have shown that the nitrogen-fixing bacteria *Sinorhizobium meliloti* 1021 can infect, colonize, and migrate within rice plants, whose growth and performance are promoted by inoculation with microbial species that increased both root and canopy growth.

Simultaneously, leaf chlorophyll levels, rates of photosynthesis, and grain yields were raised as well. Gopalakrishnan et al. (2014b) show similar effects from actinomycetes that were isolated from vermicompost in the rhizosphere of SRI plants; actinomycetes significantly enhanced total nitrogen, available phosphorous, percent organic carbon, microbial biomass carbon and nitrogen, and dehydrogenase activity over the uninoculated control. Ultimately, all of the below- and aboveground elements of crop growth were significantly enhanced over the uninoculated control.

As most beneficial soil biota function best under aerobic conditions; it becomes increasingly clear that continuously submerged fields will impair root development and the root functioning that is intimately linked to soil biota. As a consequence, nutrient uptake is negatively affected (Olaleye et al., 2001), as are root activity in terms of its active absorption area (AAA), its ability to oxidize alpha-naphthylamine, and root surface phosphatase (RSP) (Yang et al., 2004).

The greatly expanded and vigorous root systems of SRI plants will obviously enhance the opportunities for nutrient uptake from the soil (Yang et al., 2004; Zhang et al., 2009a). This has been found to apply also to micronutrient uptake and the concentration of micronutrients in the grain (Adak et al., 2015). Moreover, as discussed in Section 4.2.2, active root systems will be able to access soil nutrients more effectively from both inorganic and organic sources in the soil (Paungfoo-Lonhienne et al., 2012; Schmidt et al., 2013).

Under SRI crop management, the populations of fluorescent pseudomonads (FLPs) in the rhizosphere are increased (Suresh et al., 2014). Many of the isolates of these FLP microbes possess the ability to produce growth-promoting phytohormones (IAA and GA), siderophores (iron-chelating compounds), while facilitating solubilization of phosphate from the soil, besides exhibiting significant antifungal activity. However, increased root activity also relates to root oxidation and the production of root-sourced cytokinins (Zhang et al., 2009a). These are believed to play a major role in promoting cell division, thereby delaying senescence of the leaves (Del Pozo et al., 2005; Ookawa et al., 2004; Soejima et al., 1995; Yang et al., 2002).

Moreover, an increased root biomass, root oxidation activity, and cytokinin contents in roots are all necessary to develop an increased number of panicles and spikelets per panicle, as well as increased weights of individual grains, each of which contributes to grain yield (Yang et al., 2012). Further, aerobic soil conditions, induced by an AWD irrigation management, can significantly improve the ultrastructure of root tip cells, increase root length density, and the concentration of cytokinins as measured in root bleedings (Zhang et al., 2009a). All of these processes, essentially generated by various aerobic soil microbes, contribute positively to crop growth and yield.

Improved root functioning (i.e., under aerobic soil conditions) and as mentioned earlier in close association with soil biota, is also reflected in elevated leaf chlorophyll content and a delay in leaf senescence. Consequently, fluorescence efficiency is maintained and photosynthetic rate is increased in SRI plants as compared with flooded rice (Thakur et al., 2011). High root metabolic activity supports a higher photosynthetic rate by supplying a sufficient amount of nutrients to the shoot/leaf (Mishra et al., 2006; Mishra and Salokhe, 2010; Samejima et al., 2004; Zhang et al., 2009a).

Vice versa, actively photosynthesizing leaves ensure a sufficient supply of assimilates to the roots (and to the microbes in the rhizosphere) to maintain their functioning with the combined effect of new development and longevity of both roots and leaves.

All these interdependent relationships are referred to as the root–shoot interactions (Samejima et al., 2004). The various SRI practices (i.e., young seedlings for transplanting, wide spacing/low plant densities, organic fertilizers, and an AWD soil moisture/aerobic regime) will all affect this interaction in positive ways. Thus, the improved balance between root and shoot growth under SRI contributes directly to larger panicles, better grain setting, and heavier individual grains (as reflected in 1000-grain weight) than under conventional practices (in particular, the high plant densities and flooding). Zhang et al. (2009b) have also reported that the increased grain yields in "super" rice varieties (Liangyoupeijiu and Huaidao 9) are attributable to having an improved balance between the aboveground and belowground plant development. It follows that optimizing crop management also leads to an increased harvest index and, consequently, achieves the dual goal of increasing grain production and saving water (Yang and Zhang, 2010).

4.2.2 Plant Root–Soil Microbe Interactions: Effects on Plant/Crop Nutrition and Nutrient Uptake

Two elements, nitrogen and oxygen, are known to be crucial to plant and crop growth by affecting/regulating many intricate physiologic processes as reviewed next.

Nitrogen: With AWD irrigation and use of a (rotary) weeder, soils under SRI management will remain in a more aerobic condition than will fully submerged paddy soils. This makes the probability of nitrogen being transformed into nitrate (NO_3) rather than remaining in the ammonium (NH_4^+) form greater under SRI than under flooded conditions. Thus, Jain et al. (2013) found higher amounts of nitrate nitrogen (NO_3^-) under SRI management and more nitrogen as ammonia (NH_4^+) in flooded rice soils.

However, in addition and counter to conventional thinking, part of the soil-nitrogen will occur in organic forms such as proteins, amino acids, and peptide molecules. Such N-containing molecules in the soil are also available for uptake by plant roots (Kraiser et al., 2011; Paungfoo-Lonhienne et al., 2012). Being intermediate products of the mineralization process of organic matter by soil microorganisms, it follows that soil organic matter contents and the soil moisture regime (aerobic or anaerobic) will be important factors influencing N availability for uptake by plant roots. However, in contemporary research on nitrogen nutrition of crops, this contribution of organic-N forms has been left out of the equation. A very similar situation applies to organic-P. Certainly in the case of rice and in the context of SRI, this might prove a serious oversight.

Research by Kronzucker et al. (1999) and Kirk (2001) reported on the synergistic effects on crop growth when N is present in both NH_4 and NO_3 forms, concluding that such coprovision enhances plants' total N-uptake. A given amount of N was found to produce 40–70% more yield when provided equally in the forms of ammonium and nitrate rather than being provided only in the form of ammonium, which predominates in continuously flooded soils. This desirable pluralism of N forms is enhanced by SRI's water management practices. Also, NO_3 enhances the expression of genes for NH_4 transporters and thus the assimilation of NH_4 (Zhao et al., 2008).

Oxygen: This element has a unique role in the processes of rice growth and nitrogen utilization, which is conducive to nitrogen absorption and utilization in rice shoots (Zhao et al., 2011). Xu et al. (2013) have showed that rice seedlings with more oxygenation had higher root dry matter, longer root length, stronger root activity, and larger root absorption area compared with the roots of rice plants growing in flooded conditions. In addition, the contents of soluble sugar, as well as the enzyme activities of glutamine synthetase, glutamic acid pyruvic acid transaminase, and glutamic acid oxaloacetate transaminase, are all increased in response to aeration, indicating that aeration plays a catalytic role in ammonium assimilation and nitrogen translocation, hence it improves nitrogen absorption and utilization (Zhao et al., 2011).

Recently, it was reported that at low concentrations of nitrate (NO_3^-), NRT1.1 transporters favor basipetal transport of auxin in lateral roots, thus preventing auxin accumulation at the lateral root tips. This dynamic will slow down the outgrowth and elongation of lateral roots. However, at high nitrate conditions, NRT1.1-dependent basipetal transport of auxin is inhibited, which leads to auxin accumulation in the lateral root tip, thereby accelerating the growth of lateral roots (Krouk et al., 2010).

Although much further research is still required in these domains, it tends to confirm the importance of interactions and interdependencies between the two foundations of SRI impact: root growth and soil biota. Together the various processes, as discussed earlier, help to explain why with SRI practices, plant growth (including roots) and nutrient uptake are enhanced simultaneously. It also supports Gewin's (2010) conclusion that roots are the key to a second green revolution.

5. A PROPOSED MODEL

Based on the preceding review and interpretation of results, a model is proposed that encompasses known morphologic and physiologic changes that are responsible for raising the grain yields of rice plants grown under SRI management, shown all together in Figure 3. The model combines various practices like transplanting young single seedlings at a relatively wide spacing,

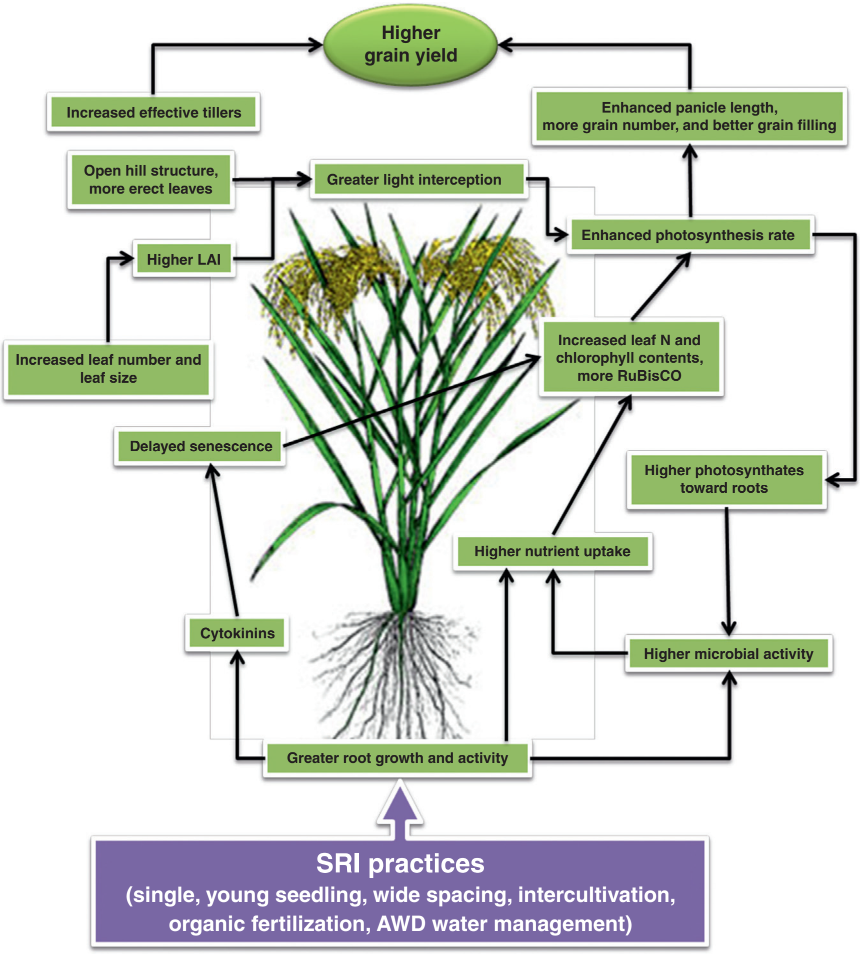

Figure 3 A schematic model showing factors that explain the increased grain yield of rice plants grown under SRI management practices. LAI, leaf area index; RuBisCO, ribulose-1, 5-bisphosphate carboxylase/oxygenase.

AWD irrigation, compost use, and weed control with a mechanical weeder (cultivator) that together lead to rice plants having profuse and active root systems. The effects of these practices are listed in Table 1.

In particular, greater root development promotes beneficial interactions with soil biota, enhancing soil microbial activity supported by higher volume and rates of root exudation into the rhizosphere. Consequently, with larger root systems the capacity of the rice plant to acquire nutrients and water and to produce growth hormones, especially cytokinins, is enhanced.

Robust root growth which favors greater cytokinin synthesis supports more cytokinin flux from the root to the shoot, which results in delayed senescence of plant leaves and prolonged photosynthetic activity (San-oh et al., 2006). Having more RuBisCO, the enzyme essential for photosynthesis, is reflected in increased levels of N and chlorophyll contents in the leaves when SRI practices are employed (Thakur et al., 2013).

Moreover, the photosynthetic rate of the plants' lower leaves is enhanced which provides an increased supply of carbohydrates to the roots, prolonging their longevity and thereby contributing to the plant's grain-filling process. At the same time, the increased tillering in SRI plants leads to more and larger leaves, and thus to an increased LAI, documented in studies of SRI such as Zhang et al. (2013). An open canopy structure with more erect leaves (minimizing the shading of lower leaves) contributes to an increased LAI which results in greater light interception during the later phase of vegetative growth and during grain formation and filling.

These phenotypic alterations of SRI plants lead to increased efficiencies of the key physiologic processes and of related beneficial interactions with soil biota. Ultimately, this is reflected in many and larger panicles that contain many more and heavier individual grains than are achieved with conventional rice cultivation practices. These multiple interacting effects are poorly reflected by studies that examine just one management practice at a time, or focus on only one effect at a time, rather than on the ensemble of causes and effects (i.e., the various interactions) which SRI practices bring about.

6. DISCUSSION: SOME WIDER IMPLICATIONS OF SRI METHODS

Considering the many calls for sustainable agricultural intensification to feed a growing world population in the future, and to achieve this under changing and less favorable climates, the SRI approach appears to offer several highly relevant advantages and new insights into the management of crops for broader benefit, to farmers, the environment, and the economy.

6.1 Implications for a Modified Agronomy

It has been reported that SRI uses 25–50% less water, while at the same time increasing yields by 20–40% or more, with higher factor productivities in comparison with conventional flooded rice cultivation methods (Jagannath et al., 2013; Kassam et al., 2011; Thakur et al., 2011; Uphoff et al., 2011). Anas et al. (2011) and Gopalakrishnan et al. (2014a) have reported that SRI practices create favorable conditions for beneficial soil microbes to prosper, improving the health, fertility, and sustainability of soil systems so that the savings in water and increases in grain yield have wider beneficial effects.

Crop yields are routinely assessed in terms of production per unit area. Thus a most efficient production is achieved by optimizing the number of plants m^{-2} without compromising individual plant performance (Thakur et al., 2010a). This implies a two-way optimization: for the community of plants and for individual plants. Practices like alternate wetting and moderate soil-drying regimes which substantially affect root growth and health will enhance water use efficiency while maintaining or even increasing grain yield. The latter is made possible by the improved canopy structure, source activity, sink strength, and enhanced remobilization of prestored carbon reserves from plant vegetative tissues into grains (Yang and Zhang, 2010).

Focusing on root systems and on the myriad creatures that live around, on, and also within plants, from microscopic life forms to visible organisms, redirects attention from the plant (solely its aboveground parts) to the whole plant (including roots) and to the ecosystems of which plants are an integral part. Indicative of agronomists' fixation on the aboveground plant is the way that they have operationalized "harvest index" (HI) as a descriptive and analytical variable. HI is defined formally as the percentage of aboveground biomass that goes into the edible portion of the plant, ignoring the roots.

It has been axiomatic in rice science, but also for wheat and other cereal crops, that the promotion of tillering *per se* is not desirable because presumably this reduces the harvest index. Instead, increasing the number of effective (panicle-bearing) tillers $plant^{-1}$ and m^{-2} has been the goal of crop breeding and management because it had been concluded that there must be a tradeoff, that is, an inverse correlation, between the number of a plant's total tillers and the number and size of its panicle-bearing tillers (Ying et al., 1998). In order to increase yields, plants were expected to allocate nutrients and photosynthates maximally to grain formation and grain-filling rather than to "waste" these on nonproductive tillers.

However, this was a zero-sum way of understanding crop performance, regarding plants as closed systems, which they are not. With SRI management, rice plants have more tillers, more roots, more leaves, longer panicles, more grains, and heavier grains as a rule. This reflects a positive-sum dynamic when plants are functioning as *open systems*. With conventional rice management, plants become, in effect, closed systems because their roots degenerate due to hypoxia and are largely inactivated by the flooding of paddies, along with the soil biota (Kar et al., 1974). Consequently, this mode of rice crop management makes the crop, with its truncated root systems, highly dependent on the exogenous provision of (inorganic) nutrients. These are used very inefficiently as only about 30–40% of the amount applied to the soil is taken up by the oxygen-deprived root systems.

As discussed already, root systems remain stunted and therefore, relatively dysfunctional under conventional practices of continuous flooding and high plant densities. SRI plants, in contrast, with their profuse and longer-lived root systems, will be more efficient in accessing soil nutrients (even when present at low concentrations as for organic-N molecules) and additionally will give the crop more resilience when coping with a range of biotic and abiotic stresses. In that respect, it is revealed that recent research on rainfed SRI rice shows that the total root mass m^{-2} from 16 SRI plants is equal to or even superior to that of 150 plants (the conventionally recommended plant density), while the SRI grain yield was greatly superior (>50%) (Thakur et al., 2015).

It follows that the profuse root systems of SRI plants have been far more efficient in accessing and utilizing nutrients at low soil-nutrient concentrations (Schmidt et al., 2013). This also places in a different perspective the high SRI yields (10–15 tons ha^{-1}) initially reported from Madagascar and achieved on soils conventionally classed as chemically very poor (Stoop et al., 2002). A logical consequence will be that the conventional mineral fertilizer applications, of which it is widely known that a large part is lost and pollutes the environment, could most likely be reduced substantially. Simultaneously, the profuse tillering contributes to increased levels of photosynthesis that benefit both the functioning of the root systems (including its nutrient uptake) and its symbiotic interactions with soil biota. As suggested already, it is this positive feedback loop that is the foundation for SRI's advantages over current rice management practices.

In this context, also the use of organic fertilizers (compost, green manure, etc.), as recommended for SRI, becomes increasingly relevant. It supplies plants with nutrients in both direct and indirect ways, serving as substrate for the soil biota that fix, cycle, and solubilize nutrients (Schmidt et al., 2013). These organic materials constitute a vital source of nutrition for the soil biota to prosper and function; thereby improving nutrient use-efficiency (Zhao et al., 2009). Organic matter amendments do more than just supply macro- and micronutrients. They simultaneously contribute to maintaining the soil structure (porosity and moisture storage capacity) that plants find crucial to root growth and to their overall development.

Only rather recently have researchers started to consider the nurturing and improvement of root systems as the key to a second green revolution, one through which yields could be increased without causing environmental damage (Ahmadi et al., 2014; Gewin, 2010). Rather than focus research efforts on developing new cultivars with robust root systems through plant breeding or biotechnological tools, SRI management promotes such root characteristics effectively through a set of agronomic practices (see Table 1). The profuse root systems that develop as a result enhance the plants' ability to overcome drought, heat, and other stresses. Perhaps even more importantly, SRI practices can succeed by using well-adapted local varieties, as well as hybrids and other improved varieties. "Unimproved" varieties have some advantages in terms of robustness under climatic stresses and meeting consumer preferences and traits. With higher market prices and greater yields under SRI management, they can expand farmers' options for profitable production.

6.2 Reductions in Greenhouse Gas Emissions

"Modern agriculture," as widely promoted by many mainstream researchers and ministries of agriculture, is highly dependent on chemical fertilizers to sustain crop yields, especially inputs of nitrogenous fertilizers. The use of N-fertilizers has increased more than 20-fold over the past 50 years (Glass, 2003), enhancing crop yield, but also becoming a major contributor to the emissions of nitrous oxide (N_2O), a more potent greenhouse gas (GHG) than methane (CH_4) or carbon dioxide (CO_2). Only 30–40% of N fertilizer applied to rice is taken up by the crop under flooded conditions. The rest is lost to the environment, causing environmental pollution, such as increasing nitrate (NO_3) levels in groundwater supplies. As present trends continue, ever more nitrogen will be released into the atmosphere and into water sources with adverse consequences (Giles, 2005; Sutton et al., 2011).

Together with the influences on plant structure and functioning, as described in the previous section, this translates into significantly higher grain yields, greater N uptake, and improved N-use efficiency under SRI as compared with conventional practices (Lin et al., 2009; Thakur et al., 2013). It is ironic that scaling back the provision of inorganic N applications can enhance rice yields, much like we see with reductions in irrigation water requirements, thereby contributing to a win–win situation in terms of both economic and environmental benefits.

Rice fields which account for 11% of the planet's arable land are notably responsible for increasing the emissions of the GHG methane, producing an estimated 10% of human-induced methane and accounting for 20% of total agricultural CH_4 emissions (Kumaraswamy et al., 2000). When soils are flooded and hypoxic, they nurture methanogens, the anaerobic microorganisms which synthesize methane. Stopping flooding will certainly reduce methane emissions, as will reductions in the application of N fertilizers. SRI practices not only reduce populations of methanogens in the soil but enhance the countervailing populations of methanotrophic bacteria (Rajkishore et al., 2013).

The use of organic fertilization in combination with midseason drainage, two practices followed under SRI, demonstrably mitigate methane emission from rice fields (Yan et al., 2009). Although under unflooded conditions, as with SRI management, more nitrous oxide (N_2O) might be released by the activity of nitrifying and denitrifying bacteria under aerobic soil conditions; this effect is likely to be meager in view of SRI's reducing applications of inorganic N. Several studies have shown no increase or nonsignificant increases in N_2O with SRI management, as noted later.

Empirical measurements of GHG emissions and estimates of their respective impacts on global warming potential (GWP) are bound to vary widely because of the volatility and variability of the soil microbial communities that are responsible for the generation of GHGs and their sensitivity to differences in soil structure, temperature, and moisture (Setiawan et al., 2014). Nevertheless, researchers in several countries have tried to assess the respective levels of GWP associated with different management systems for irrigated rice.

In India, several studies on GHG emissions in relation to SRI management have been conducted. In Andhra Pradesh state, a direct comparison between SRI and farmer practice was made by Gathorne-Hardy et al. (2013). With SRI crop management, GHG emissions (considering CO_2, CH_4, and N_2O all in terms of CO_2 equivalence) were calculated to be >25% less per hectare than with standard practices. Per kg of paddy rice produced, emissions were >60% less because of the higher SRI yield. Also in India, Jain et al. (2013) report that from SRI fields using recommended fertilizer rates (both organic and inorganic fertilizers), the N_2O emission increased by 22.5% as compared with conventional flooded rice. Yet, with CH_4 emissions reduced by 61–64%, the overall GWP effect was calculated to be 28% lower for SRI than for conventional transplanted rice. Suryavanshi et al. (2013) also reported lowest CH_4 emission and GWP from SRI fields and the highest from conventional transplanted flooded rice. Researchers in Korea have calculated a 65–73% reduction in GHGs from SRI-managed plots as compared with conventional flooded plots (Choi et al., 2014).

Given the number of factors involved, measurements on GHG emissions are likely to be quite variable, so at best one can only calculate ranges, not absolute values. Even so, there is already good reason to expect that SRI management methods will mitigate the dynamics making for adverse climate change, and that this will not occur at the expense of reduced food production.

6.3 Crop Resilience in the Context of Climate Change

Climate variability with more frequent and severe droughts, floods, storm damage, cold snaps, untimely rains, and hot spells is a major threat to agriculture. To achieve a more productive and resilient agriculture requires major shifts in the way that land, water, soil, nutrients, and genetic resources are managed to ensure their efficient and sustainable use (FAO, 2013). Reducing GHG emissions per unit of land and/or agricultural product and also increasing carbon sinks would contribute to the mitigation of climate change.

As described in Section 4, SRI management practices induce substantial changes in plant characteristics. Most notably among these are more profuse root systems, stronger and thicker stems, as well as thicker leaves that all contribute to the crop’s resilience against droughts, lodging due to strong winds, storms, and heavy rainfall, as well as pest and disease infestations, respectively (Chapagain et al., 2011; Dill et al., 2013; Uphoff, 2011). These changes are first and foremost a result of the greatly reduced plant densities (16–25 plants m^{-2} in SRI and 150 or more plants m^{-2} in conventional systems). Paradoxically, reduced seed rates (just 1/5th or even 1/10th of conventional practice) are a major contributing factor to the SRI effect of higher yield. More research should be done on how modified rice phenotypes, from any variety, can better withstand biotic and abiotic stresses which will predictably become greater with climate change. But there is already enough evidence of such effects that agronomists should take a greater interest in these relationships.

7. CONCLUDING OBSERVATIONS

Essentially, SRI practices create more favorable soil–water–plant–-rhizosphere relationships than are possible under conventional wetland rice production with its continuously flooded fields and hypoxic soil conditions as well as its close crowding of plants above- and belowground. There is a growing body of research evidence that supports the inference that the improvements in grain yield under SRI practice result from improved morphologic and physiologic features of the rice plant, both in root and shoot organs.

SRI practices improve the growth of roots and their activity, favoring water and nutrient uptake. These changes support higher rates of photosynthesis and delayed senescence of the leaves. Also, the open canopy structure, more erect leaves, larger and thicker leaves, and greater leaf area demonstrably improve light interception by the canopy, even with much-reduced plant populations. At the same time, there is greater abundance and activity of beneficial soil organisms in the rhizosphere and, it may be inferred, in the plants (Anas et al., 2011).

All these phenomena, interlinked and interdependent, lead to significant improvements in rice plants' yield-contributing characteristics and ultimate yield under SRI methods. These processes are apparently enhanced by supportive bacteria, fungi, and other beneficial soil organisms in combination with the profuse root systems. These potentially important, yet complex relationships all merit much further research.

Studies on the benefits that can derive from symbiotic microbial endophytes that reside in plants are just beginning. The phenotypic changes that result from SRI crop management are, probably not coincidentally, similar to those that have been observed experimentally and reported in the literature as attributed to increased populations and activity of soil organisms (bacteria, fungi, actinomycetes, and mycorrhizae). These constitute influential parts of the plant–soil microbiome. This has health and growth benefits for plants that are parallel to those of the human microbiome for people (Uphoff et al., 2013).

Given the constraints of growing water scarcity with concomitant pressure to produce more grain – that is, to achieve more crop per drop – SRI is a promising option for rice growers, more attractive than most other, presently available methods of rice cultivation. SRI offers an agroecological and climate-smart form of agriculture that integrates economic, social, and environmental dimensions of sustainable development, jointly addressing the challenges of food security and dealing with climate constraints.

Many plausible explanations for the impacts of SRI practices on rice phenotypes are available from the current scientific literature, as reviewed in the present article. SRI, however, still raises many more research issues than can be answered from the available literature. Consequently, it should still be regarded as "a work in progress."

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