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Improving the phenotypic expression of rice genotypes: Rethinking “intensification” for production systems and selection practices for rice breeding



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ABSTRACT

Intensification in rice crop production is generally understood as requiring increased use of material inputs: water, inorganic fertilizers, and agrochemicals. However, this is not the only kind of intensification available. More productive crop phenotypes, with traits such as more resistance to biotic and abiotic stresses and shorter crop cycles, are possible through modifications in the management of rice plants, soil, water, and nutrients, reducing rather than increasing material inputs. Greater factor productivity can be achieved through the application of new knowledge and more skill, and (initially) more labor, as seen from the System of Rice Intensification (SRI), whose practices are used in various combinations by as many as 10 million farmers on about 4 million hectares in over 50 countries. The highest yields achieved with these management methods have come from hybrids and improved rice varieties, confirming the importance of making genetic improvements. However, unimproved varieties are also responsive to these changes, which induce better growth and functioning of rice root systems and more abundance, diversity, and activity of beneficial soil organisms. Some of these organisms as symbiotic endophytes can affect and enhance the expression of rice plants' genetic potential as well as their phenotypic resilience to multiple stresses, including those of climate change. SRI experience and data suggest that decades of plant breeding have been selecting for the best crop genetic endowments under suboptimal growing conditions, with crowding of plants that impedes their photosynthesis and growth, flooding of rice paddies that causes roots to degenerate and forgoes benefits derived from aerobic soil organisms, and overuse of agrochemicals that adversely affect these organisms as well as soil and human health. This review paper reports evidence from research in India and Indonesia that changes in crop and water management can improve the expression of rice plants' genetic potential, thereby creating more productive and robust

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phenotypes from given rice genotypes. Data indicate that increased plant density does not necessarily enhance crop yield potential, as classical breeding methods suggest. Developing cultivars that can achieve their higher productivity under a wide range of plant densities—breeding for density-neutral cultivars using alternative selection strategies—will enable more effective exploitation of available crop growth resources. Density-neutral cultivars that achieve high productivity under ample environmental growth resources can also achieve optimal productivity under limited resources, where lower densities can avert crop failure due to overcrowding. This will become more important to the extent that climatic and other factors become more adverse to crop production. Focusing more on which management practices can evoke the most productive and robust phenotypes from given genotypes is important for rice breeding and improvement programs since it is phenotypes that feed our human populations.

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1. Introduction

There is certainly need for continued improvement in the genetic potentials of rice varieties, as such potentials can yield greater returns on the land, labor, capital, seeds, water, and other inputs that farmers invest in their rice production. Also, plant breeding can increase the range of options available to farmers. However, we suggest here that more attention be given to ways in which rice varieties (genotypes) can be managed more beneficially, to induce the fuller phenotypic expression of their genetic potentials and obtain more robust and more productive plants.

This suggestion reframes somewhat the tasks of plant breeding for proved rice performance, given that observed phenotypes do not map directly to genotypes, reflecting environmental influences as much as genetic endowments. When breeders use phenotypic expression and yield performance under test-site conditions for their screening and selection, their efforts will be more efficient and successful to the extent that these decisions are informed by a fuller understanding of environmental influences on phenotypic expression and of the associated mechanisms of such influences. We need to double the world's rice production by 2050 [1]. Achieving this ambitious goal will require realizing more effective agronomic expression of

the genetic potentials that exist in rice cultivars, beyond the gains that can still be made in raising rice potentials through various methods of plant breeding.

Data presented in Table 1 show the increases in rice yields at the national level that have been achieved over the past five decades in 10 countries that produce over 85% of the world's rice: Bangladesh, Brazil, China, India, Indonesia, Myanmar, Pakistan, Philippines, Vietnam and Thailand, calculated from FAO and USDA sources available on IRRI's website [2].

Between 1960 and 2010, these countries achieved, on average, a 150% increase in paddy rice yields, an impressive accomplishment. These gains were based in large part on the breeding of new, improved varieties and on national programs to exploit these greater genetic potentials, although credit must go also to rice farmers for their efforts and adaptations to raise their respective levels of productivity. More was required than just better, more productive genes for higher yield.

It is evident from inter-decade comparisons of crop performance that there has been a *deceleration* in the improvement of yields since the 1980s. Rice yields in these 10 countries increased, on average, by 23.2% during the decade of the 1980s; however, this rate of increase declined to 19.3% for the 1990s, and then to 16.5% for the 2000s (Table 1).

Table 1 – Country paddy yields ($t\ ha^{-1}$), 1959–2011, three-year averages from FAO and USDA statistics.^a

| Country | 1959–1961 | 1969–1971 | 1979–1981 | 1989–1991 | 1999–2000 | 2009–2011 | 5-decade increase (%) |
|--------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------------------|
| Bangladesh | 1.67 | 1.70 | 1.89 | 2.59 | 3.77 | 4.20 | 151 |
| Brazil | 1.69 | 1.34 | 1.46 | 2.14 | 3.25 | 4.53 | 176 |
| China | 2.03 | 3.30 | 4.28 | 5.62 | 6.32 | 6.60 | 225 |
| India | 1.53 | 1.67 | 1.86 | 2.62 | 3.01 | 3.30 | 116 |
| Indonesia | 1.93 | 2.38 | 3.53 | 4.33 | 4.38 | 4.36 | 126 |
| Myanmar | 1.65 | 1.71 | 2.45 | 2.85 | 3.14 | 3.29 | 100 |
| Pakistan | 1.36 | 2.24 | 2.41 | 2.32 | 2.95 | 3.28 | 141 |
| Philippines | 1.21 | 1.65 | 2.23 | 2.79 | 3.10 | 3.64 | 200 |
| Thailand | 1.65 | 1.93 | 1.85 | 2.10 | 2.60 | 2.83 | 71 |
| Vietnam | 1.94 | 2.07 | 2.15 | 3.18 | 4.25 | 5.44 | 180 |
| Average yield | 1.67 | 2.01 | 2.41 | 2.99 | 3.57 | 4.15 | 149 |
| Increase during the decade (%) | – | 20.4 | 19.4 | 23.2 | 19.3 | 16.2 | – |

^a For a review of increases in rice productivity over the past five decades, we analyzed yield statistics ($t\ ha^{-1}$) for the past ten decades from the ten countries that have the highest production of rice (86% of the world's total), found in IRRI's online rice statistics data base [2]. Three-year averages were calculated for the start and the end of each decade to smooth out year-to-year variations, and data from FAO and USDA were averaged to account for the differences in annual average yield reported from these two sources. The decadal averages are unweighted to reflect the variations in country experience, because otherwise the trends in India and China would dominate the statistics.

This deceleration was noted already in the 1990s, first by IRRI researchers [3] and then by FAO analysts [4]. The latter reported that the annual growth rate for rice yield during the 1960s was 2.51%, then 1.76% during the 1970s and 2.80% during the 1980s, but only 1.10% in the 1990s (through 1996). By the late 1990s, IRRI scientists concluded from their analysis of rice yield data that the yield potential of tropical rice had remained relatively constant for several decades, at around 10 t ha^{-1} [5]. Indeed, they found that the average yield from IRRI's most popular high-yielding variety, IR-8, had declined by about 2 t ha^{-1} over the preceding three decades.

This prompted an effort to breed for what was called “the new plant type” (NPT), an attractive concept that, however, has not achieved the expectations set for it [6–8]. The NPT strategy aimed to raise the yield potential of rice by breeding plants with fewer tillers, only 8–10 each, but with all of them becoming fertile [9]. Little consideration was given in the crop modeling on which this strategy was based to the fact that rice plants with fewer tillers will have a concomitant reduction in their numbers of roots, given that tillers and roots originate synchronously from the same meristematic tissue.

Breeding efforts were directed toward increasing rice plants' harvest index (HI) rather than to improving their root systems [10]. Neglect of the ontogenetic connection between the development of plants' tillers and roots could account for NPT's inadequate source capacity, which did not match its greater sink capacity. Although NPT plants had more spikelets than high-yielding varieties (HYVs), they also had less grain filling [8]. Moreover, since NPT trials were conducted with 14-day-old seedlings, planted singly in a square pattern $25 \text{ cm} \times 25 \text{ cm}$ [10], it is not clear how much of the yield increase recorded in the NPT trials was due to genetic gains and how much to modifications in crop management. In any case, there has been little discussion of the NPT in recent years, with no mention of NPT research in IRRI's annual reports beyond 2008.

The reduction in the rate of rice yield increase that has occurred since the 1980s represents a phenomenon that economists know as diminishing returns. This phenomenon occurs when, as the scale and/or intensity of an activity increases, there is declining benefit or output produced from each additional unit of input. This inverse relationship, ubiquitous for most processes of industrial or agricultural production, may well apply to the prevailing paradigm for contemporary agricultural research and crop improvement. In the nature of things, the payoff from conducting research according to a given set of assumptions, concepts, and methods is likely to diminish and attenuate over time, needing new thinking to revitalize the activity and to achieve more rapid gains in productivity. This universal tendency cautions against assuming that “more of the same” will necessarily be successful and calls for openness to new perspectives and new directions in rice research.

2. Realizing better phenotypic expression of genetic potentials

For decades, much research to raise rice production has focused on making genetic improvements in rice cultivars,

and crop management research has been undertaken principally to capitalize on advances in plant breeding rather than being regarded as a factor in crop production that could raise rice yields through its own innovations. As rice plants were bred and selected to become more responsive to increased inputs of fertilizer, water, and agrochemicals, research focused on ways in which these inputs could be used most efficiently with the improved varieties.

Yet improvements in genetic potential and crop management are inseparably complementary, as symbolized in the well-known equation: $P = f(G + E + G \times E)$, where P stands for phenotype, G and E respectively represent genetic potential (genotype) and environmental influences, and the interaction term $G \times E$ refers to their joint effects. This paper suggests that in order to meet our global rice production goals, as well as for rice farmers to achieve better returns from their efforts, more attention should be directed to ways in which crops' growing environments can be modified, both above and below ground, to capitalize more effectively on a whole range of $G \times E$ interactions.

Our perspectives here are informed by our research on and learning from a crop management methodology known as the System of Rice Intensification (SRI). Adaptive use of its recommended methods has achieved yield increases and other agronomic, economic and social benefits in over 50 countries, beyond what farmers have obtained when they grow any given variety (genotype) with their usual practices, and even with what are currently recommended management practices (RMP) [11].

SRI is still controversial in some circles, and it is true that when SRI reports were first rejected in a series of critical articles that appeared in the middle 2000s [12–15], there was little published evidence on SRI results and mechanisms, except for Uphoff and Randriamiharisoa [16]. The supporting scientific evidence for SRI claims is, however, now quite extensive, with the published literature on SRI extending to over 600 articles, including many in top peer-reviewed journals [17].

One problem in evaluating SRI is that its results reported in the literature vary considerably, and sometimes widely, especially between on-station and on-farm results. This variability has been disconcerting for many scientists, although most evaluations have confirmed the initial published presentation on SRI [18]. It has become increasingly evident that SRI's variability stems largely from its results' not deriving from a particular genetic “blueprint” or from the application of certain kinds and amounts of fertilizer. If results can be attributed primarily to genes or to agrochemical inputs, one would expect them to be relatively fixed or proportional. SRI effects, in contrast, range rather widely, suggesting that some other causal factors are involved.

SRI's mechanisms diverge considerably from those of the Green Revolution, as its results derive from making changes in plants' growing environment. The operative factors appear to be particularly (a) the growth and functioning of profuse and longer-lived root systems, and (b) the mobilization of beneficial services from soil organisms, including the plant-soil microbiome [19,20]. These effects—larger, better functioning, less-senescent root systems, and a more abundant, diverse and active soil biota—result from specific recommended

modifications in crop management practices. Being biologically (and especially microbiologically) driven, the influence of these two factors on the productivity of rice phenotypes can be quite variable, even volatile, as seen below.

Controversy over SRI may still continue for a while, and certainly much remains to be studied and learned about the respective practices and their effects. More research is needed on SRI's mechanisms, conditions, vulnerabilities and limitations. But as many as 10 million farmers are already using and benefiting from SRI ideas and methods on ~4 million hectares of lowland and upland rice area in Asia, Africa and Latin America. Over the past half dozen years there have been few published challenges to SRI, so the controversy is receding. It is appropriate to focus on what can be learned from SRI experience and research for meeting the world's daunting rice production goals in the decades ahead.

A major barrier to the scientists' acceptance of SRI thinking and results has been that some of the "super-yields" reported contradicted prevailing thinking about maximum biological yield potentials for rice based on crop modeling exercises. The concept of a "yield ceiling" assumes a primacy of G vis-à-vis E , with maximum yield in a given growing season made dependent in models on a certain level of solar radiation and the thermal environment, with these relationships essentially genetically determined. Yoshida [21] calculated that in the tropics, there is a dry-season yield ceiling (or limit) of 15.9 t ha^{-1} . This figure became widely cited and accepted, and it made reports of any yield that surpassed this level appears impossible or 'unscientific'.

Yet the possibility of there being "outliers" should not be rejected out of hand, especially favorable outlying yields. Outliers are, by definition, not common, and they are certainly not the norm. But they deserve attention as possibly giving clues to making further improvements in agronomic yield. People are fed not by outliers but rather by averages. However, to feed more people, we need to raise present averages in the direction of desirable deviation from the present norm.

With the System of Rice Intensification (SRI) in its original, "classic" form, crops of irrigated rice are established by transplanting very young seedlings, 8–12 days old (less than 15 days), singly (rather than in clumps of 3–5 plants), and in a square grid pattern, with wider spacing, usually $25 \text{ cm} \times 25 \text{ cm}$ (optimum spacing can be more or less than this, depending on soil quality and other conditions). Surprisingly, even with SRI plant populations reduced by 80% to 90%, this wider spacing, in combination with the other SRI practices, gives farmers higher yields. The much-improved plant phenotypes show greater root growth and tillering, as discussed in the next section, and greater resilience, not discussed here, which result in greater and more assured yield. See [22] for evidence from China on resistance of SRI-grown rice plants to biotic and abiotic stresses.

Other SRI practices include: (a) no continuous flooding of the rice paddies, so that soil is maintained in mostly aerobic condition; (b) weed control with a mechanical weeder, hand or motorized, that actively aerates the soil, further promoting root growth and aerobic soil biota; and (c) supplementing soil systems with as much organic matter as possible, to support larger, more diverse and more active populations of beneficial soil organisms. These practices and explanatory principles for SRI derive from the work of Henri de Laulanié during the

1960s, 1970s, and 1980s in Madagascar [23]; but they have since been successfully adapted through locally formulated practices to improve rainfed rice production [24] and to raise the yields of a variety of other crops [25].

SRI methods have been particularly effective when used with high-yielding varieties and hybrids: all SRI yields over 15 t ha^{-1} have been achieved with improved cultivars, high-yielding varieties (HYVs), or hybrids. But SRI methods are also effective with "unimproved" traditional varieties, boosting their yields to 5 to 10 t ha^{-1} and sometimes more. Such yields can give farmers a good return on their resources, given that traditional varieties of rice often command a higher market price because of consumer preferences. Thus, with SRI management, local varieties can be more profitable than modern varieties, depending on relative yields and market prices. To obtain the highest yields, however, the merits of improved genetic potential are repeatedly confirmed by SRI experience.

A paddy yield of 22.4 t ha^{-1} reported from Nalanda district in Bihar state of India in November 2011 has been controversial because skeptics did not know that the yield had been properly measured by Department of Agriculture technicians using standard methods [26]. What has been overlooked in the debate over one farmer's super-yield was that four of his neighbors, other farmers in Darveshpura village who also used SRI methods on one-acre fields in that season, also achieved paddy yields that matched or surpassed the previous world record from China—19.0, 19.2, 19.6, and 20.2 t ha^{-1} . These farmers planted in that season a Bayer hybrid, Arize 6444, although the highest yield was grown with the Syngenta hybrid 6302 [26].

Omitted from this published report was that these five Darveshpura farmers who achieved SRI "super-yields" in *kharif* 2011 also planted these same hybrid varieties on other parts of their farms during that season. The yields from these hybrid genotypes, managed with standard recommended practices, were between 5.9 and 6.5 t ha^{-1} . Although these were certainly respectable yields, 2 to 3 times the usual paddy yield in Bihar state, they were much lower than achieved with SRI practices from the same genotypes under the same soil and climatic conditions. These results showed how much difference can be made by modifying crop management based on SRI principles to make fullest use of $G \times E$ interactions to help farmers achieve desired higher yields.

The reports of these unprecedented yields in Bihar resulted in controversy in the press and in the blogosphere [27,28]. Hardly any attention was paid to an even higher yield two years later, 23.8 t ha^{-1} , produced by a farmer in Tamil Nadu state on a half-acre SRI field near Madurai [29,30]. This record yield was achieved with an iconic, long-duration, improved variety, CR 1009, released by Tamil Nadu Agricultural University in 1982, and reported by TNAU breeders to have high tillering ability with high yield potential. They assessed its yield potential as 6 t ha^{-1} [31], only a quarter as much as the farmer in this case was able to elicit from this improved genotype when he managed it with SRI practices. Agronomic "yield ceilings" are thus not something that is intrinsic just in the plant's genes. Rather they reflect $G \times E$ interactions of the plant with a variety of ecophysiological and environmental influences [32].

A meta-analysis of Chinese research evaluations of SRI compared to what researchers considered to be best management practices (BMP), assessing 64 pairs of data from 17 published studies has found that even with not all of the recommended SRI practices being used, basic SRI management outperformed BMP by more than 10% on average [33]. If minimal SRI was used—that is, only a few practices—the result was 4% lower average yield than with BMP. However, “good” SRI methodology using many of the practices gave >20% higher yield than BMP, and full use of the practices could produce >30% more than BMP, contradicting [14] and [15].

Best SRI results, as we understand them, derive from maximizing the physiological and developmental potentials of rice plants as a whole, growing under mostly aerobic soil conditions, supported by (a) the growth of large, effective root systems and (b) a beneficial soil biota that interacts with the roots and the whole plant system. (b) is harder to assess than (a), but is probably more fundamental to success, given that (b) can have positive effects on (a), as shown by Yanni et al. [34]. These factors, taken together, lead to plants that can achieve more efficient growth and development, with greater resilience when challenged by biotic and abiotic stresses.

3. Evidence of improved phenotypic responses of rice plants to SRI practices

Whether SRI practices can induce significant differences in rice plant phenotypes—in their physical organs and in their physiological performance—has been questioned in the literature [14,15], but this challenge was not based on the results of any detailed experimental trials that could test whether or not certain claims about phenotypic improvement were correct.

The kinds of trials needed to assess SRI claims of improved phenotypes were started in 2005, prompted by published critiques of SRI, at the Directorate of Water Management in Bhubaneswar, part of the Indian Council for Agricultural Research. This section presents data from these trials that have been reported in the literature [35–37], but not brought together for systematic overview and comparison. All the trials were with same-variety rice plants grown using either SRI management practices or currently recommended management practices (RMP). The practices evaluated were those posted, respectively, on the websites of SRI-Rice at Cornell University, Ithaca, NY, USA (<http://sri.cals.cornell.edu/>) and India’s Central Rice Research Institute in Cuttack (<http://www.crrl.nic.in/>).

The respective sets of plants were grown in the same soil, under the same climatic conditions, and with the same fertilization. This latter factor was not assessed in the evaluation, even though there is reason to believe that fully organic fertilization used with the other SRI practices can give better crop performance than inorganically fertilized plants [16]. The trials were all performed with random block design and with replications as reported in detail in the referenced articles [35–37].

All of the plots in this four-year series of experiments had integrated nutrient management; that is, a combination of organic and inorganic fertilizers. No attempt was made to optimize plant nutrition. Thus, soil amendments were treated in these trials as a constant, with no variation in the amounts and kinds of fertilization. The research was designed to see what, if any, physiological and morphological effects would result from careful transplanting of seedlings that were young and more widely spaced, thereby reducing plant density in the field (by sixfold), also with water management that maintained the soil under mostly aerobic conditions, and with weed control measures that actively aerated the surface soil layer.

In these on-station, controlled trials, it was found that SRI methods enhanced yield on average by 48% compared with RMP, not varying soil nutrient management. This increase was attributable to the many changes in morphological and physiological characteristics of SRI plants that are reported below, in comparison with rice plants grown from older seedlings that were more crowded and experienced continuous flooding. Tables 2 and 3 summarize the growth, morphological and physiological improvements that were observed in plant phenotype when rice plants were grown with SRI methods compared with conventional, flooded management.

Table 2 – Effects of rice management practices on morphological characteristics of roots, tillers, leaves, and canopy structure in rice.

| Parameter | Management practice | | | Increase with SRI (%) |
|---|---------------------|--------|---------------------|-----------------------|
| | SRI | RMP | LSD _{0.05} | |
| <i>Root growth parameters below ground</i> | | | | |
| Root depth (cm) | 33.5 | 20.6 | 3.5 | 63 |
| Root dry weight (g hill ⁻¹) | 12.3 | 5.8 | 1.3 | 112 |
| Root dry weight (g m ⁻²) | 306.9 | 291.8 | NS | 5 |
| Root volume (mL hill ⁻¹) | 53.6 | 19.1 | 4.9 | 111 |
| Root volume (mL m ⁻²) | 1340.0 | 955.0 | 180.1 | 40 |
| Root length (cm hill ⁻¹) | 9402.5 | 4111.9 | 712.4 | 129 |
| Root density (cm ⁻²) | 2.7 | 1.2 | 0.2 | 125 |
| <i>Tillers, leaves and canopy structures above ground</i> | | | | |
| Plant height (cm) | 124.2 | 101.4 | 8.1 | 22 |
| Culm height (cm) | 84.0 | 67.5 | 4.3 | 24 |
| Tiller number hill ⁻¹ | 18.3 | 8.9 | 3.5 | 106 |
| Tiller number (m ⁻²) | 450.1 | 441.2 | NS | 2 |
| Tiller perimeter (cm) | 2.9 | 2.1 | 0.3 | 38 |
| Leaf number (hill ⁻¹) | 79.8 | 35.6 | 15.8 | 124 |
| Leaf number (m ⁻²) | 1997.6 | 1766.5 | 229.4 | 13 |
| Leaf length (cm) | 65.25 | 48.14 | 6.09 | 35 |
| Leaf width (cm) | 1.82 | 1.34 | 0.21 | 35 |
| Flag leaf length (cm) | 39.45 | 30.27 | 4.49 | 30 |
| Flag leaf width (cm) | 2.10 | 1.66 | 0.31 | 27 |
| Leaf area index (LAI) | 3.95 | 2.60 | 0.28 | 52 |
| Specific leaf weight (mg cm ⁻²) | 5.50 | 4.89 | 0.34 | 13 |
| Canopy angle (°) ^a | 33.1 | 17.8 | 3.6 | 86 |

Source: Thakur et al. [36].

^a Canopy angle was measured with a protractor using the following equation: CA (in degrees) = 180 – (θ₁ + θ₂), where θ₁ and θ₂ are the angles of inclination of the outermost tillers from a horizontal orientation on both sides, measured at flowering stage.

Table 3 – Effects of rice management practices on root functions, physiological parameters and N uptake in rice.

| Parameter | Management practice | | | Increase with SRI (%) |
|--|---------------------|--------|---------------------|-----------------------|
| | SRI | RMP | LSD _{0.05} | |
| Amount of exudates (g hill ⁻¹) | 7.61 | 2.46 | 1.45 | 209 |
| Amount of exudates per m ² (g m ⁻²) | 190.25 | 122.95 | 39.72 | 55 |
| Exudation rate per hill (g hill ⁻¹ h ⁻¹) | 0.32 | 0.10 | 0.06 | 220 |
| Exudation rate per m ² (g m ⁻² h ⁻¹) | 7.93 | 5.12 | 1.66 | 55 |
| Leaf elongation rate (LER) (cm day ⁻¹) | 5.97 | 4.45 | 0.21 | 36 |
| Chlorophyll a (mg g ⁻¹ FW) | 2.35 | 1.68 | 0.14 | 40 |
| Chlorophyll b (mg g ⁻¹ FW) | 1.02 | 0.90 | 0.07 | 13 |
| Total chlorophyll (mg g ⁻¹ FW) | 3.37 | 2.58 | 0.11 | 30 |
| Chlorophyll a/b ratio | 2.32 | 1.90 | 0.29 | 22 |
| F _w /F _m ratio | 0.796 | 0.708 | 0.017 | 13 |
| Φ _{PSII} | 0.603 | 0.486 | 0.020 | 24 |
| Transpiration (m mol m ⁻² s ⁻¹) | 6.41 | 7.59 | 0.27 | 19 |
| Leaf temperature (°C) | 34.48 | 33.09 | NS | 4 |
| Net photosynthetic rate (μmol m ⁻² s ⁻¹) | 23.15 | 12.23 | 1.64 | 89 |
| N uptake (kg N ha ⁻¹) ^a | 77.4 | 51.0 | 8.6 | 52 |

^a Measurements were taken after harvest. Source: Thakur et al. [35–37].

We will discuss some of the factors that could account for the observed and measured differences.

Root studies of the respective crops showed clearly different patterns of growth between SRI and RMP methods. As seen in Table 2, the effective root depth, total root length, and dry weight per hill recorded were markedly greater in SRI plants than for their RMP counterparts. Root dry weight was not found to be significantly different on a unit-area basis, not surprisingly, given the sixfold difference in plant density. The proportion of roots that were brown or black—that is, non-functional and decayed or decaying—was observed to be significantly greater in plants from continuously flooded RMP plots than in those that experienced alternate wetting and drying (AWD) irrigation for SRI.

SRI practices thus not only induced greater root growth, but also enhanced root activity, evident from the greater xylem exudation rates measured in our study. Another effect of greater and deeper root systems in SRI was enhanced nutrient uptake [37,38]. Continuously submerged rice plants, in contrast, have impaired root development that reduces nutrient uptake [39,40].

SRI practices were seen to enhance rice plants' growth and tillering ability, improving both their plant and culm height and increasing the strength of their tillers as reflected in greater tiller perimeter. This latter difference is consistent with findings that have documented the greater resistance to lodging of plants grown with SRI methods [22,41].

Owing to their early establishment, SRI plants suffer much less from what is called transplanting shock. Subsequent,

more favorable growing conditions then allow the plants to complete a greater number of phyllochrons before the onset of anthesis, so that they produce a greater number of strong tillers and larger root systems than RMP plants.

In contrast, RMP plants appear to be constrained by reduced growth vigor and by competition for nutrients, space, and light during the later stages of their vegetative growth. This constraint was indicated by a reduced rate of increase in the RMP plants' growth beyond 60 days after germination, seen in Fig. 1. This reduction can be attributed to SRI plants' lower leaf senescence, which may be due in turn to larger amounts of cytokinins (root exudates) being transported from the roots, as discussed below.

The number and size of leaves at the flowering stage were significantly greater in SRI plants than in RMP plants, leading to a higher leaf area index (LAI) under SRI than under RMP. The extensive root systems developed by SRI plants enhanced their water and nutrient uptake, resulting in greater leaf elongation rates (LER), 6 cm day⁻¹ compared with only 4.5 cm day⁻¹ under RMP, probably a factor contributing to the larger SRI leaf size. The higher specific leaf weight (SLW) in SRI plants, also reported in Table 2, indicates that they had thicker leaves than those of rice plants grown under RMP [36].

RMP plants manifested a more compact aboveground structure, with tillers that were more vertical and less horizontal. In contrast, SRI plants had a more "open" architecture, as measured in terms of greater canopy angle. SRI tillers splayed out more widely and thus covered more ground area. Greater leaf area index (LAI) and a more favorable canopy structure facilitated greater canopy light distribution and more light interception in the SRI crop beyond 50 days after germination (DAG) as seen in Fig. 2. At panicle initiation, the respective rates of light interception for SRI and RMP plants were 89% and 78%, representing a 15% advantage for SRI-grown rice [36].

SRI plants exhibited darker, greener leaves, indicative of their higher chlorophyll content, having a higher Chl a/b ratio than conventionally managed rice, as seen in Table 3. This color difference indicated a better nutrient supply received by the SRI hills than the RMP rice hills. Our studies also showed

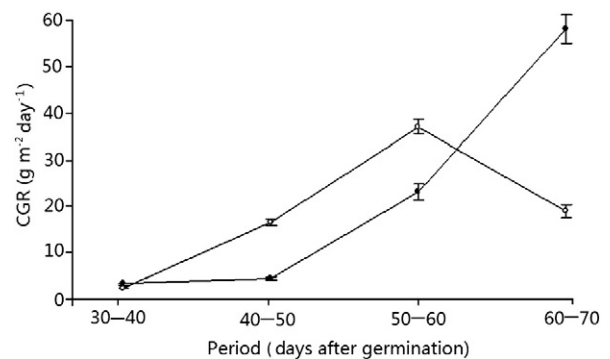


Fig. 1 – Changes in crop growth rate (CGR) during the vegetative stage of rice grown with SRI and RMP practices. Closed and open circles represent SRI and RMP management, respectively.

Vertical bars represent SEM ± (n = 6).

Source: Thakur et al. [36].

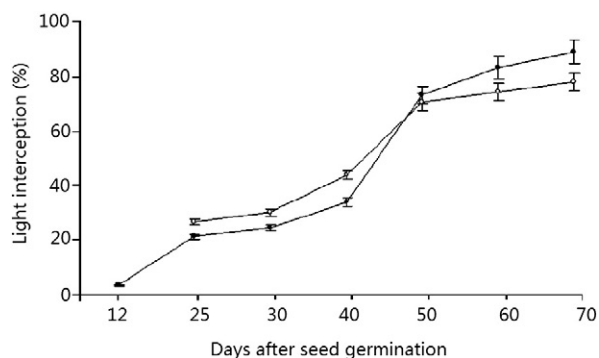


Fig. 2 – Changes in light interception by the canopy during vegetative stage in rice grown with SRI and RMP practices. Closed and open circles represent SRI and RMP management, respectively. Vertical bars represent SEM \pm ($n = 6$). Source: Thakur et al. [36].

that SRI leaves had a higher light utilization capacity (F_v/F_m and Φ_{PSII}) and a greater unit leaf-surface photosynthetic rate, especially during the reproductive and ripening stages of the crop, also shown in Table 3. Actively photosynthesizing leaves ensure a sufficient supply of assimilates to the roots for their development and longevity, thereby supporting active root functioning.

At the same time, greater root metabolic activity supports a higher rate of photosynthesis by supplying sufficient amounts of nutrients to the shoot and its leaves. This interdependence relationship has been referred to as root–shoot interaction, and SRI practices have a substantial effect on it. Interestingly, a high photosynthetic rate with lower CO_2 concentration inside the substomatal cavity in SRI plants (Table 2) also suggests that SRI plants have a more efficient carboxylation system, similar to that in C_4 plants.

The instantaneous water-use efficiency of the leaf (represented by the ratio of photosynthesis rate to transpiration rate) is a measurement of the carbon gained through photosynthesis per unit of water transpired. The higher unit surface-photosynthesis rate in SRI plants coupled with their lower transpiration indicates that they use water more efficiently than do RMP plants. The latter fixed $1.6 \mu\text{mol } CO_2$ per mmol water transpired, whereas the SRI plants synthesized more than twice as much carbohydrate relative to water utilization, $3.6 \mu\text{mol } CO_2$ per mmol of water [35].

Higher root growth and activity under SRI management is associated with increased root oxidation activity and more root-derived phytohormones, in particular cytokinins [42]. The latter are believed to play a major role in promoting cell division, which delays the senescence of leaves. Delaying senescence means maintaining higher levels of leaf chlorophyll content, which in turn gives greater fluorescence efficiency, reflected in the higher photosynthetic rates in SRI plants than in flooded RMP rice.

The combined effects of these measurable morphological and physiological differences between rice plants grown with SRI vs. RMP practices contribute to SRI's greater biomass, yield, and factor input productivity. There are also reports of

enhanced robustness to the effects of climate change (water stress in particular), but this response was not studied in these trials.

The improved growth and functioning of roots and shoots under SRI management contributed directly to larger SRI panicles (more spikelets per panicle), better grain setting (higher percentage of filled grains), and heavier individual grains (higher 1000-grain weight). There was a 48% yield enhancement on average, with nutrient amendments held constant. Differences in these parameters are reported in Table 4.

Our measurements showed a considerably higher harvest index (HI) for the SRI rice plants; that is, more grain relative to shoot biomass, although this is not a consistent effect. Zhao et al. [40] reported a similarly higher HI from evaluations in China. However, Barison and Uphoff [39] found in Madagascar research that the SRI plants there produced their higher yield without an increase in HI, as all components, roots, canopy and grains, expanded roughly proportionally under this improved management. This finding warrants further research.

Many of these same differences have been documented in similar research undertaken at Bogor Agricultural University (IPB), a national university in Indonesia. These results were reported in posters prepared for the 4th International Rice Congress in Bangkok, October 2014, comparing a variety of physiological and morphological parameters in the roots and shoots of rice plants grown from the same variety. Significant differences were measured in the growth of root hairs, in root length, root dry weight, and aerenchyma (air pockets), although no significant difference was found in root respiration [43]. Above ground, SRI crop management methods were associated with significant differences in leaves' chlorophyll levels and their rates of photosynthesis, in the uptake of N and P to the leaves, in panicle length, and in grain filling; but no significant differences were found in plants' transpiration rates or leaf temperature [44]. Beneficial changes in rice plants' morphology and physiology through favorable modifications in their environments above and below ground have been repeatedly seen; for example, the effects that alterations

Table 4 – Effects of rice management practices on yield-contributing characteristics, grain yield, straw weight and harvest index.

| Parameter | Management practice | | | Increase with SRI (%) |
|--|---------------------|-------|---------------------|-----------------------|
| | SRI | RMP | LSD _{0.05} | |
| Panicle number hill ⁻¹ (ave.) | 16.9 | 6.9 | 3.5 | 145 |
| Panicles (m ⁻²) | 439.5 | 355.2 | 61.6 | 24 |
| Panicle length (cm) (ave.) | 22.5 | 18.7 | 2.3 | 20 |
| Number of spikelet panicle ⁻¹ | 151.6 | 107.9 | 12.9 | 40 |
| Filled spikelets (%) | 89.6 | 79.3 | 5.1 | 13 |
| 1000-grain weight (g) | 24.7 | 24.0 | 0.2 | 3 |
| Grain yield (t ha ⁻¹) | 6.51 | 4.40 | 0.26 | 48 |
| Straw weight (t ha ⁻¹) | 7.28 | 9.17 | 1.19 | -21 |
| Harvest index | 0.47 | 0.32 | 0.04 | 47 |

Source: Thakur et al. [36].

in their growing environment can exert on rice plant roots [45–47].

Benefits achievable through modified management do not diminish the value of further efforts to enhance the genetic potentials of rice. As discussed in Section 2, all of the highest yields achieved with SRI methods to date have been with “improved” varieties, HYVs, or hybrids. The implication of what we have been seeing and measuring with SRI management modifications is that plants’ growing environments should be considered as an intrinsic part of plant breeding efforts, not as something separate from or secondary to improvements in the genome. A further implication is that crop breeding can benefit from insights from SRI experience and evaluations, which should make efforts for genetic improvement and growing-environment optimization more congruent and convergent.

4. Implications for rice breeding and crop improvement: an alternative selection approach

During the latter part of the 20th century, the ambitious breeding and selection efforts made to improve the yield potential of rice crops produced an annual genetic gain in the range of 0.5% to 1.0% [48]. Such a rate of increase, however, will not be enough for meeting the escalating global demand for food to support a global population that is projected to reach 9 billion by 2050 [1]. More rapid progress in crop breeding, contributing thereby to higher levels of rice production, will require innovative approaches that address and resolve certain problems and limitations that are associated with “classical” methods of plant breeding.

Maximizing selection efficiency is important for screening accurately for overall phenotypic expression, as well as for greater tolerance to various biotic and abiotic stresses. Selection efficiency signifies the capability to select unique plant genotypes based on their phenotypes, and is reflected in annual rates of genetic gain. Unsuccessful phenotypic selection of best genotypes denotes reduced selection efficiency.

Four main factors have hindered selection efficiency in crop breeding and selection programs: (i) inter-plant competition, (ii) soil heterogeneity, (iii) genotype-by-environment [$G \times E$] interactions, and (iv) heterozygosity. These have been previously identified and discussed by Fasoula and Fasoula [49–51]. To these factors can be added another: (v) the effects of the soil biota on rice plant phenotypes, which will be discussed more in Section 5. This fifth factor could be subsumed under the first and/or second factors listed above, because soil organisms are affected by (i) and contribute to (ii).

We will focus on the discussion of inter-plant competition because this has such strong effects on the phenotypes among which breeders select when working on genotypic improvements. Competition interferes with the equal sharing of growth resources among plants, having the effect of (a) decreasing crop yields and (b) reducing selection efficiency [49,51]. In addition, it contributes to a decrease in a cultivar’s yield over time, as will be discussed. An example of such cultivar deterioration, propagated under the “classical” conditions of

inter-plant competition, is the history of the high-yielding rice variety IR8, released by the International Rice Research Institute (IRRI) in 1968. Data from Peng et al. [5] show that the average yield from IR8 has declined by some 2 t ha^{-1} over the past 30 years.

Although decline in cultivars’ yield over time is common, its cause has not been resolved within the plant breeding discipline. Two factors that can contribute to cultivars’ diminishing yield over time are inter-plant competition and an inverse relationship between plants’ abilities to yield and to compete [49,51,52]. At the individual plant level, it is seen that plants carrying genes for higher yield potential also carry genes that confer lower competitive ability, and vice versa; plants with genes for lower yield potential will carry genes for higher competitive ability [49,53]. This established inverse relationship between yielding and competitive ability has been proposed as one overlooked reason for farmers’ “traditional” practice of replacing their seed of landraces and cultivars since ancient times [54,55]. This is based on their observation that lower yields result if seed is not replaced after several generations.

Research studies have showed that the reproduction of cultivars in dense stands year after year favors a gradual proliferation of plants within the gene pool that are low yielders but strong competitors. These proliferate at the expense of those plants that are higher yielders but weaker competitors, thus contributing to a decline in the yield potential of the whole set of cultivars over time [49–51]. The selection of phenotypes under dense-stand conditions will favor choosing plants that are lower yielders/stronger competitors [49,51]. Current selection methods, which do not address this bias in phenotypic selection under high plant density, reduce selection efficiency and present a methodological impediment to further advances in plant breeding and crop improvement.

4.1. A prognostic strategy for crop breeding

An alternative strategy for crop improvement called “prognostic breeding” has been the gradual outcome of several research studies, summarized in [56], which sought to overcome the limitations of classical selection and screening strategies. These strategies have produced limited genetic gains, as noted above. The research data on which this alternative breeding and selection strategy is based are, not coincidentally, consistent with the results of the SRI crop management reported above. In this prognostic system, wider spacing between plants promotes each plant’s optimal phenotypic expression of its genetic yield potential, in part by reducing inter-plant competition and in part by producing stronger plants that have more robust shoot and root systems.

To address the causes of reduced selection efficiency of the “classical” breeding strategies and to overcome the barriers that are limiting year-to-year genetic gains, one needs to take account of: (1) the conditions that maximize crop yield and selection efficiency, (2) the genetic components of crop yield potential, (3) the conditions under which these genetic components can be measured reliably, and (4) the role of production environments and $G \times E$ in the selection of “champion” plants. We discuss here why prognostic breeding considers these factors crucial for the

efficient identification of “champion” plants that truly represent genotypic advances.

4.1.1. Conditions that maximize crop yield and selection efficiency
Competition, defined as the unequal sharing of growth resources among plants caused by genetic and acquired differences, will reduce crop yield and selection efficiency in plant breeding [49,51]. It follows that crop yield is maximized when all the plants in a field share the growth resources equally, are uniform, and are producing the same (for them highest) yield.

To accomplish this ideal, several agronomic and genetic measures have been identified as essential for reducing acquired and genetic competition [49,51,57]. Agronomic measures include the establishment of fields which reduce acquired-competition traits by having ample and evenly distributed resources for growth as well as synchronous seed germination, growth, and development of the plants. The genetic measures include the development of highly buffered monogenotypic cultivars (hybrids, inbred lines, or clones) to eliminate genetic competition among plants. Genetic competition reduces overall crop yield, given that plants' respective competitive advantages fail to compensate for their competitive disadvantages.

One of the reasons that SRI practices give overall higher rice yields is that they reduce greatly the acquired competition among rice plants by transplanting younger seedlings instead of older ones. This practice promotes more uniform growth and development of plants in the field than is possible with conventional methods of rice cultivation. Certainly using only one seedling per hill instead of 2–3 together reduces competition between root systems below ground and between canopies above, thus producing a plant that can optimally express its genetic yield potential and its tolerance to biotic and abiotic stresses. The even spacing of plants in all directions further reduces acquired competition and results in higher yields than with conventional practice.

The negative effects of competition on crop yield explain the predominance of monogenotypic over polygenotypic cultivars. The negative effects of competition on selection efficiency explain why the evaluation of plants should be performed at ultra-wide plant spacing, taking account of and counteracting the established negative correlation between plants' yielding and competitive abilities [49,51].

When breeders make their selections for yield and stability under conditions of high plant density, they favor poor plants that are stronger competitors/lower yielders rather than the reverse: superior plants that are higher yielders/weaker competitors [49]. Classical selection strategies that use densely grown plots accordingly fail to select effectively for highest yield since they favor plants that have been bred for “competition” genes rather than “productivity” genes. This reality creates a constraint on doubling or tripling the desired (and needed) annual rates of genetic gain for rice and other crops.

To remove this constraint, prognostic breeding [56] uses as the unit of selection the individual plant grown at ultra-wide plant spacing, where phenotypic expression among plants, including root and shoot development, is maximized, and where rapid and vigorous early plant growth along with

desired tolerance to stresses is incorporated into the plant breeding process, increasing selection efficiency and genetic gain.

A fairly basic but misleading assumption needs to be addressed. Classical breeding methods assume that when traits enhanced by competition are to be selected for, the evaluation of plants under competition is essential for successful selection. But this assumption needs reexamination, since the success of phenotypic selection does not depend on conditions that increase the absolute value of a trait, but rather on those that optimize the *range* of phenotypic expression of the trait [50]. The range of phenotypic trait expression is maximized only when the plants are grown at ultra-wide plant spacing [49–51], where the genetic potential of each plant is fully expressed and where plant phenotypes develop a strong tillering capacity and a deep and extensive root system, as with SRI management.

Our research has shown that high plant density is not a prerequisite for attaining high crop yields, meaning that a crop's yield maximization can occur over a wider range of plant densities [50,56]. This finding suggests that plant breeders should not perform selection with stands as dense as the conventional common practice dictates. This conventional wisdom is a misunderstanding in classical breeding practice, where selection is performed under conditions of high plant density. Because of the inverse relationship between yielding and competitive ability already discussed [49,51], this type of selection does not result in the most productive and stable plant phenotypes.

In contrast, selection of plants for high yield and stability in the absence of inter-plant competition will permit the selected genotypes to perform well under various densities in farmers' fields, including under conditions where the original planting density is modified during the season; for example, when plant emergence is not uniform or when drought stress strikes [50,56]. The prognostic strategy for crop breeding enables the development of cultivars that are not dependent on a specific density and that can exploit lower seeding rates to ensure harvestable crop yields when resources are limited, such as under drought stress.

In contrast to classical breeding methods that use low selection pressures (10–20%), prognostic breeding uses ultra-high selection pressures (2.0–0.5%), to select fewer “champion” plants and to accelerate gene fixation [56]. Imposition of high selection pressures is essential for maximizing selection efficiency, but it can be accomplished only when single plants are grown at ultra-low plant densities. When plants are grown at high plant densities, the inverse relationship between the ability to yield and to compete confounds selection for highest plant yield. In such instances, “champion” plants cannot be reliably identified and phenotypic selection becomes less effective. Thus, in classical breeding methods, only lower selection pressures can be used and selection efficiency is reduced.

4.1.2. The genetic components of crop yield potential

After the individual plant is established as the unit of selection for crop yield potential, it becomes crucial to partition the assessment of crop yield into genetic components. We have initially analyzed crop-yield genetic potential into three components: genes that control plant yield, genes that

control yield stability, and genes that control plant adaptability [50]. As a second step, justified below, we can reduce the components of crop-yield potential to two: genes controlling plant yield and genes controlling stability, by replacing progeny lines with sibling lines [56,58].

This reduction paves the way for evaluating the crop yield potential of individual plants in every generation by assessing the product of *plant yield* \times *yield stability*. Prognostic breeding permits an evaluation for yield genes and stability genes within the same generation by evaluating the crop yield potential of each plant through its siblings rather than in successive generations [56]. Comparison among sibling lines offers several advantages, the key one being that individual plants can be evaluated *concurrently* on the basis of the two components of their yield potential: the plant yield potential as measured by the plant yield index $[PYI = (x/\bar{x}_r)^2]$ and the plant's stability of performance, measured by the stability index $[SI = (\bar{x}/s)^2]$ of the sibling line to which the plant belongs.

The stability of performance of individual plants can be assessed through either their progeny or their siblings. Progeny evaluation used by classical breeding methods can be accomplished only in consecutive generations and years, whereas sibling evaluation is accomplished in the same generation and year, markedly increasing the efficiency of selection and reducing the time required to release a cultivar.

The plant prognostic equation $[pPE = (x/\bar{x}_r)^2 \cdot (\bar{x}/s)^2]$ is used to measure the crop yield potential of each plant and to select crop-yield "champion" plants that will generate the sibling lines of the generation to come [56]. The two components of crop yield cannot be evaluated objectively, however, unless we can address the confounding effects of soil heterogeneity on single-plant yields through the use of advanced experimental design.

4.1.3. The conditions under which the genetic components of crop yield can be measured reliably

The barriers created by soil heterogeneity for evaluating accurately the two components of the crop yield potential can be overcome by use of experimental designs that are called "honeycomb selection" designs [59]. In such designs, the unit of selection is the individual plant grown in the absence of competition, using ultra-wide plant spacing.

These designs have some unique properties and can be used to evaluate any number of sibling lines (D) given by the formula $D = X^2 + Y^2 + XY$, where X and Y are whole numbers from zero to infinity [59]. The properties of these designs are illustrated using as an example the replicated D-31 honeycomb design shown in Fig. 3, which is set up to evaluate plants of 31 sibling lines. Plants of these lines are placed symmetrically within the field so that every plant of any line being evaluated is located in the center of a moving complete replicate, as shown by the gray circles for two random plants of line 11 in Fig. 3.

This layout permits effective reduction of the aberrant effects of soil heterogeneity on single-plant yields by using the plant yield index $[PYI = (x/\bar{x}_r)^2]$, where x is the yield (in g) of any plant, and \bar{x}_r is the mean plant yield (g) of all the surrounding plants within the moving circle or ring [56,58]. This yield index measures the plant yield potential devoid of the confounding effects of soil heterogeneity.

Plant stability of performance is evaluated simultaneously by the stability index $[SI = (\bar{x}/s)^2]$, where \bar{x} is the mean plant yield and s is the standard deviation of the sibling line to which the plant belongs [56]. Selection for stability of performance is accomplished through the effective exploitation of soil heterogeneity by placing plants of each sibling line in a triangular grid pattern spreading across the whole field, as shown for plants of line 11 in Fig. 3.

The triangular grid, a unique property of the honeycomb designs, is formed for plants of all lines to be evaluated in the design. It capitalizes on the effects of soil heterogeneity by distributing plants of each sibling line symmetrically across the entire field. The two parameters: the plant yield index, measuring plant yield potential, and the stability index, measuring plant stability of performance, are used in the plant prognostic equation to measure the crop-yield potential of each plant: $pPE = (x/\bar{x}_r)^2 \cdot (\bar{x}/s)^2$. These two components of crop yield select for density-neutral cultivars, by selecting simultaneously for the lower and the upper limit of optimal plant density.

This selection property is important, because the two limits are controlled by different categories of genes. Selection for plant yield extends the lower limit of optimal plant density, while selection for stability of performance extends the upper limit of optimal plant density, since it is selecting for tolerance to various biotic and abiotic stresses [50,51,57].

Tolerance to high-density planting is the direct outcome of selection for tolerance to various environmental stresses. Since biotic and abiotic stresses are always present in fields, the designs provide an accurate way to select for plants' tolerance to environmental stresses, and, as a result, for their tolerance to high plant density also. Consequently, because selection in prognostic breeding is performed on single plants grown at ultra-wide plant spacing, the developed cultivars, being density-neutral, can be grown at a wider range of plant densities in farmers' fields.

4.1.4. The role of the production environments and $G \times E$ in the selection of "champion" plants

The role of the breeder is to develop objective phenotypic criteria of evaluation and selection, bearing in mind that the genome is capable of exploiting constantly changing agro-ecological conditions by triggering its self-restructuring mechanisms for adaptation and evolution [56,58]. Production environments, which shape phenotypic expression, can range from highly productive to less productive to severely drought-stressed, to characterize one range. In any case, when the criteria of evaluation and selection are objective, they can be used to select "champion" plants reliably for both favorable and marginal environments.

Each production environment will support a unique set of "champion" plants that are able to exploit its particular agro-ecological conditions. It is noteworthy that self-restructuring mechanisms, which are triggered by $G \times E$ interactions that are different in each environment, cannot be accurately reproduced in the laboratory or the greenhouse.

Self-restructuring mechanisms can trigger genetic and epigenetic changes in response to environmental stimuli, even within homogeneous gene pools [50,60]. Rasmusson and Phillips [61] have reported that elite gene pools have inherent

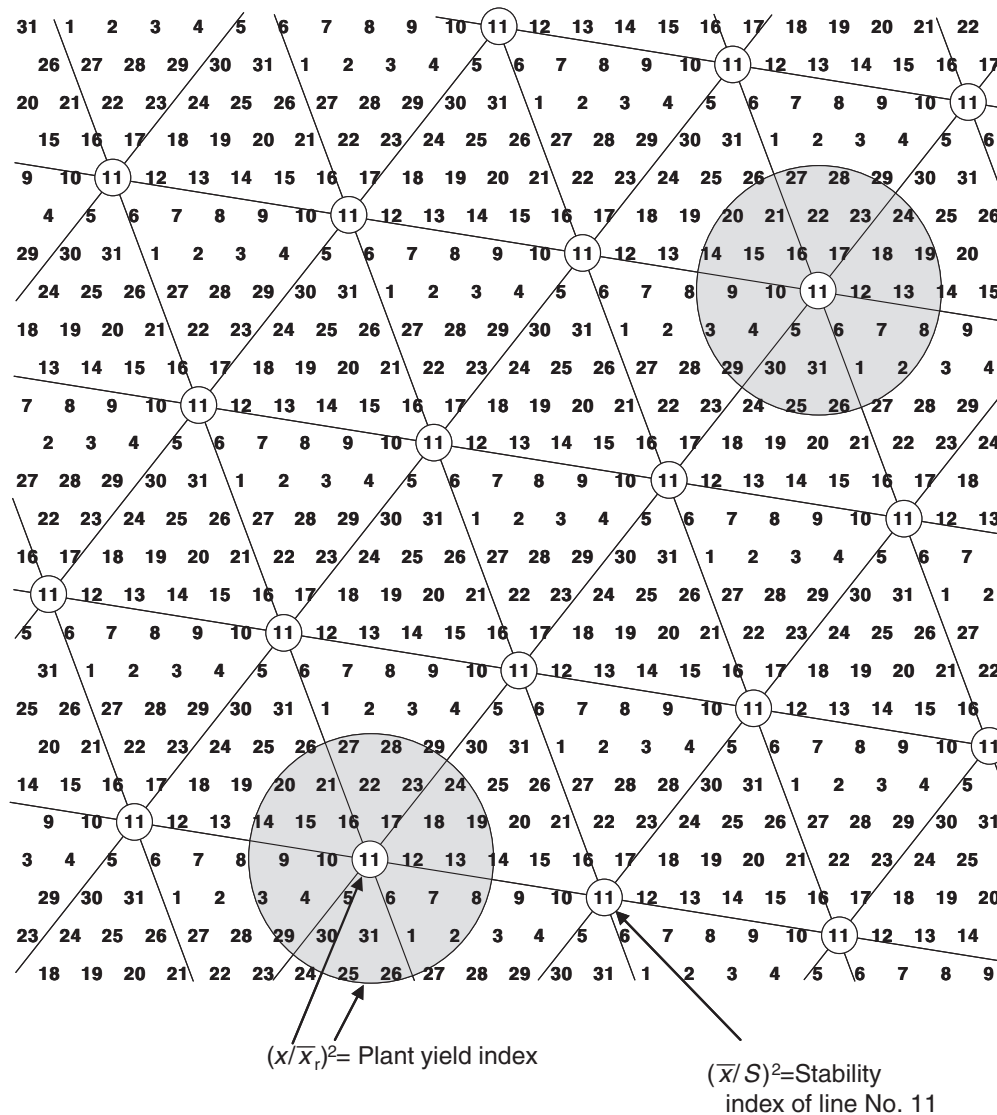


Fig. 3 – The replicated D-31 honeycomb design which evaluates the plants of 31 sibling lines. Each plant is located in the center of a complete moving replicate, shown for two random plants of line 11 (gray circles). The plant yield index (PYI) measures the plant yield devoid of the confounding effects of soil heterogeneity (x is the yield of the central plant, and \bar{x}_r is the mean plant yield of all the surrounding plants within the circle or ring). The stability index (SI) measures accurately the stability of each sibling line by taking advantage of soil heterogeneity through the formation of the triangular grid that allocates plants uniformly across the whole field. The grid is shown here for plants of line 11.

mechanisms to provide a continuing source of new genetic variation, to cope with changing environmental challenges. It is possible that genetic and epigenetic changes triggered in response to the different production practices promoted by SRI are responsible for some of the higher yields and improved yield components recorded with SRI vs. so-called best management practices. This area constitutes a promising field of research. Given that prognostic breeding has developed objective criteria for evaluation and selection, the selection of “champion” plants with high crop yield according to this methodology is not visual, but rather a matter of quantitative calculation, thus making it amenable to automation.

4.2. The importance of developing density-neutral cultivars in rice

Prognostic breeding can be used in rice to develop true-to-type breeding lines and hybrids that are density-neutral. The role of high plant density in crop-yield maximization has been a stumbling block that plant breeders have largely overlooked. Classical breeding strategies have considered high plant density a necessity for maximizing crop yield potential [62]. However, prognostic breeding has provided evidence that high plant density is not a prerequisite for achieving high crop yields, meaning that crop yield maximization can occur under a wider range of plant densities [50,51,56].

Density-neutral cultivars do not require higher planting densities to give maximal yield per hectare, but can do so at lower densities, provided that weeds are managed efficiently. These cultivars can perform well under limited growth resources (such as water), where the use of lower plant densities may avoid crop failure from overcrowding and may optimize crop yield under adverse conditions. At the same time, they can perform well under ample environmental growth resources where higher planting densities can be used.

Development of density-neutral cultivars in rice offers distinct advantages. These cultivars compete effectively against weeds by having rapid early growth that covers the field before the majority of weeds emerge and that reduces the light available for weed growth. Their competitive ability against weeds is also attributable to their deep and extensive root systems that confer tolerance to drought [49,50]. We note that what is being improved is not the genetic competitive ability of the cultivar, but its ability to have rapid early growth and cover the field before the majority of weeds emerge.

Density-neutral cultivars are better equipped to exploit marginal environments by use of lower planting rates in conformity with the availability of resources [56]. This means that crop yield can be optimized even when environmental resources are limited, leading to more sustainable production. Density-neutral cultivars are ideal for SRI crop and water management that can effectively support lower plant populations and reduced water demand. That plants of modern rice cultivars have not been intentionally developed to grow and yield well under a wide range of plant densities may explain some of the yield variation that has been found in research studies with SRI management.

Optimal results will be produced when the cultivars used in SRI cultivation are density-neutral and can exploit effectively the conditions favoring lower plant populations, which are likely to be forced upon more and more rice farmers as a result of climate change. It is our experience that rice cultivars with profuse tillering capacity tend to be density-neutral and are able to produce high crop yields when lower plant populations are used. This is a reason why the Indian improved rice variety CR1009, released in 1982 in Tamil Nadu and showing high tillering ability and high yield potential, was able to produce a record yield of 23.8 t ha⁻¹ with SRI practices [30].

5. Importance of the plant-soil microbiome for crop performance

Complicating the challenge of making the best selections of “champion” plants for improving rice genotypes through plant breeding is the growing realization that plants, despite appearances, do not develop as autonomous organisms. Their genes do not determine their destiny through $G \times E$ interactions with a largely inert environment. Rice, like other plants, can be better understood as *systems* rather as *organisms* by themselves. What we consider as the “plant” is their visible manifestation, but there is much that is unseen. Plants in fact depend for their existence and success upon uncountable multitudes of microorganisms that live around, on, and inside them, in their tissues and even in their cells.

We now know that human beings have about 10 times as many microorganisms living in and on their bodies as all of the *Homo sapiens* cells that make up their bodies [63]. This human microbiome is paralleled for plants by what is called the plant microbiome or phytomicrobiome [19], which might be better referred to as the plant-soil microbiome [20] because the microorganisms that inhabit and influence the growth and health of plants, indeed specifically of rice, are also resident in the soil and move between soil and plants, having mostly beneficial effects on the growth of plants’ roots and shoots, and consequently on crop yield [64,65]. The rhizosphere, which has long been characterized as the soil immediately around plant roots, extends beyond the roots’ surface (the rhizoplane) and functionally into the roots themselves [66]. Plants’ epidermal cells below and above ground provide a protective barrier in many but not in all respects.

Microorganisms move into and out of plants much more freely and frequently than previously imagined. As plants have co-evolved with them for >400 million years, microorganisms have established multiple mutualistic and symbiotic relationships that are ultimately more important than the deleterious relationships that are scientifically much better known. There has been more than a century of microbiological research on pathogens and parasites, but only a few recent decades of examining how and why plants are so dependent upon and interdependent with the invisible microbial universe which is essential for plants’ growth and health. Only in recent years have advanced analytical methods been developed, such as proteomic and transcriptome analysis, which can demonstrate and begin to explain the intimate connections between the plant kingdom and the preceding domains of the bacteria, fungi and archaea [67]. This brief section calls attention to the fact, not yet fully appreciated, that the phenotypes chosen by breeders for genetic improvement are not just a function of the crops’ genetic traits or of the plants’ growing environment which is now mostly characterized in chemical and physical terms, but also of the multiplicity, diversity and activity of soil organisms.

It is fairly well understood that microbes modify the soil environment for better or for worse, affecting the soil’s structure and its functioning through processes and effects like soil aggregation and porosity, water retention, and nutrient cycling and availability. The success of crop plants in such environments is also affected by less well-understood relationships, such as induced systemic resistance that confers endogenous protection from within the plant against damage from pathogens and pests, as reviewed by Pieterse et al. [68].

Less known but very important are research findings that the presence of soil organisms in the tissues of plants’ roots, sheaths and leaves as symbiotic endophytes can lead to the up- and down-regulation of specific genes in the cells of these organs [64,65]. These microbially induced modifications in the expression of genetic potential strongly affect plants’ capabilities in specific ways, such as levels of chlorophyll and rates of photosynthesis in the leaves, and rates of respiration and water use efficiency in the plant, as the ratio of photosynthesis to transpiration [64]. Evidence of such alterations in the physiology of SRI-grown plants was presented in Section 3.

Thus, when apparently superior plants are selected for breeding purposes, it is not certain without microbiological and molecular investigation whether or to what extent their improved phenotypic performance, rather than being primarily a function of their genotype, has been affected by the inhabitation of plant organs by microorganisms that otherwise reside in the soil [69]. Now that these invisible relationships are becoming known, an understanding of this microbiological dimension of crop plants' growth, health, and productivity needs to be factored into plant breeding strategies and methodologies. Although we have no direct evidence, there are reasons to think that the super-yield performances discussed in Section 2 reflect a mobilization of the advantages and services that the plant–soil microbiome can confer on plants when the environmental conditions (temperature, moisture, substrates, etc.) are optimized for the growth of beneficial microorganisms both in the soil and on and in the plant. These conditions are a result of crop management decisions that affect the crowding of plants vs. their wider spacing for root and canopy growth; the anaerobic vs. aerobic conditions of the soil and rhizosphere; and the paucity vs. abundance of nutrients not just for the plants but for the organisms, micro to macro, that constitute the soil food web [70].

Dealing with the influences that the soil biota has on plant performance adds an unwelcome degree of complexity to the tasks of plant breeders. But it also opens up some important new possibilities that need to be explored and exploited, jointly by breeders, agronomists, microbiologists and others, if we are to achieve the tremendous increases in rice production that are needed over the next 30–40 years.

6. Discussion: intensification options and plant breeding strategies for raising rice production

The preceding sections have reviewed an approach to the intensification of rice systems that is less dependent on the use of external inputs to elicit higher outputs of grain. This result is made possible by mobilizing biological processes and potentials that are present in the rice genome and in the biota of healthy soil systems. We have considered also a strategy for plant breeding that corresponds with and can enhance the modified management strategy proposed.

This analysis suggests that improved cultivars be regarded less as a sole or primary cause of greater crop yields and more as part of an ensemble of genetic and management changes that move rice production toward the twin objectives of productivity and sustainability. More attention is given to crops' growing environments, rather than focusing so predominantly on their genes. Also, more weight is given to E factors and $G \times E$ interactions, reframing crop research to consider more fully the roles and contributions of root systems and the soil biota. Raising the harvest index (HI), which has been a prime objective of plant breeding efforts, is de-emphasized with more attention to the ways in which the structure and functioning of root systems and soil systems can be improved through combinations of breeding and management innovation. Large and vigorous root systems are considered as assets rather than as liabilities, as implied by the current objective of maximizing harvest index. Attention is shifted from genotypes as

independent variables to phenotypes as dependent variables, to be optimized through a variety of research initiatives and development interventions. This effort involves multiple disciplines, but especially microbiology, which is assuming ever more importance for our understanding of the domains of flora, including rice, and of fauna, including ourselves.

The discipline of plant breeding has advanced considerably over the past 60 years, moving beyond its initial assumptions about double-helix, base-pair determinism to appreciate that "junk DNA" is not junk at all. That term reflected our lack of knowledge of the material to which it referred, now better designated by the residual category of noncoding DNA. There is increasing understanding of the manner in which the phenotypic expression of rice genotypes derives cumulatively from the growing conditions provided to individual crop plants, affecting their biomass growth and their phenological development, their root and shoot morphology, their yield both in quantity and quality, and all of the components of yield. As the molecular processes that underlie and implement phenotypic expression become better understood, we see that they explain only the most proximate causation, not plant ontogeny in any fundamental sense.

Most rice cultivation since the 1950s has been based on the assumption that higher yields are mainly the result of higher inputs of synthetic mineral fertilizers being provided to genetically improved plants that are better able to convert these chemical inputs into biological products. It was further assumed that to obtain higher yields, the unit rate of photosynthesis could not be altered, so that increased yields would come only from increasing the harvest index, achieved by dwarfing the rice plant's aboveground structure to make its grains a relatively greater proportion of crop biomass, at the same time packing as many plants as possible in a unit of area. This prescription of high seed rate and high plant population density, along with higher mineral fertilizer loading of soils, however, resulted in weaker plants that were more vulnerable to biotic and abiotic stresses [71]. It also increased the levels of water and environmental pollution and contributed to diminished soil health, as well as to the degradation of crops' genetic yield potential, as discussed in Section 4.

It has also been assumed that the biotic stresses that emanate from insect pests, pathogens, and weeds and the abiotic stresses arising from changes in crops' biophysical conditions can best be addressed by making crop genetic improvements, aligned with the application of synthetic agrochemical biocides of various kinds. Rice agronomy and water management studies became tied to the crop breeding objectives and selection practices derived or deduced from the assumptions discussed above. The control of insects, pathogens, weeds was attempted through the introgression of genetic resistance together with biocide applications. It was not considered that the recommended crop management practices could themselves be contributing to the greater incidence of pests and diseases and to crops' vulnerability to abiotic stresses [72].

SRI as an alternative management-based strategy has proceeded in different directions. One always wants to start a rice crop with the best genetic material available, as this practice yields the highest returns on inputs of land, labor, capital and water. But for some purposes and in some

circumstances, what is the best genotype for a farmer may not be an “improved” variety. Considerations of grain quality, resistance to endemic stresses, input availability, costs of production, and resulting productivity all need to be weighed. The possibility that higher paddy output can be attained with some reduction in material inputs, rather than through their increase, is now credible as the higher productivity of land, labor, seed, water and/or capital under SRI crop management has now been observed in over 50 countries (<http://sri.ciifad.cornell.edu/countries/index.html>), and the scientific explanations and justifications for this management strategy are accumulating more and more. Recent research reported from China shows SRI management practices reducing both rice crops’ susceptibility to sheath blight and to lodging, as these practices produce more resilient phenotypes [22].

It should not be surprising that preoccupation with G in crop improvement R&D has been accompanied by diminishing returns, as seen in Table 1. The experience and analyses reported in this review make a strong argument for treating G × E interactions as a more central and explicit part of research strategies and crop improvement programs, and in agricultural development at the farm and landscape level. SRI principles are now being applied also to crops other than rice, such as wheat, millet, and sugarcane [73]. This extension indicates that SRI concepts and practices offer some general relevance for agricultural research, both for breeding and for crop and soil science.

Consequently, the term “intensification” should be understood as including the promotion of interactions between and among plants, soil, water, nutrients, and soil organisms, both in space and in time, within cropping systems and in broader production systems. This need not be the only kind of intensification; agriculture is not a monolithic enterprise. This version of intensification aims to create conditions for growth that enhance productivity and resilience more than can other forms that depend heavily on applications of synthetic agrochemical inputs.

Similarly to the ecological intensification opportunities represented by SRI methods, Conservation Agriculture (CA) has shown that ecological methods favoring the development and maintenance of healthy soils with active soil biota, larger root systems, and diversified cropping can lead to profitable intensification of production and improved resource-use efficiency and resilience. They offer a different, more hospitable growing environment than with most current soil and crop management practices that are heavily dependent on tillage [73–75].

CA principles are consistent and compatible with those of SRI crop and water management. These two systems for crop, soil, water, and nutrient management can be combined to generate greater agronomic, ecological and socioeconomic benefits. This combination is beginning to occur in agroecological settings where the potentials of CA and SRI together have been perceived by development stakeholders, including adaptive mechanization to reduce the labor requirements for SRI practice and also to save more water [76,77].

Agroecological methods such as SRI and CA for production intensification—by better managing and mobilizing existing genetic potentials within plants and the soil systems in which they grow—offer opportunities to promote sustainability for farmers both large and small, but particularly for smallholders

who are often resource-poor and have little access to new knowledge and technical support. These methods enable small farmers to raise their production without having to rely on purchased inputs, improving their livelihoods by better use of locally available resources. At the same time, with appropriate adaptations, larger farmers who can afford the use of external inputs can achieve substantial environmental as well as economic benefits by optimizing the use of these inputs within agroecologically informed production systems [76]. This approach can make them part of the solution to global challenges rather than contributors to our growing environmental problems.

There is an urgent need for scientists, donor agencies, and international institutions to rethink the concept of “intensification”, bringing environmental and ecological considerations into the planning and conduct of research for rice and other crop improvement. Plant breeding can be an important part of this emergent strategy by incorporating more G × E thinking into the planning and conduct of research and by recognizing the role that the microbiome plays in shaping the phenotypes that emerge from genotypes, whether improved or unimproved.

Increased attention to G × E interactions has implications for the way in which we approach cropping systems and farming systems, seeking the best mixes of crops, soil, nutrients, water, pests, energy, equipment and machinery, labor and other inputs, and managing these resources within a landscape framework across space and time. The aim is to meet multiple objectives of sustainable production and ecosystem services at the respective levels of crop, cropping system, farm, landscape, community and region. Breeding and other crop improvement programs should be taking advantage of a much larger set of G × E opportunities than at present. This will enable them to maximize, with minimum—that is, optimized—reliance on external inputs, plants’ phenotypic expression from a range of genotypes within cropping systems that contribute to sustainable productivity, resilience, ecosystem services, and livelihoods.

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