



REVIEW ARTICLE

Direct-seeded rice in India: A sustainable transition in cultivation practices

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Abstract

In the era of climate change, declining freshwater availability and rising labour costs are driving the search for alternative management systems to enhance grain yields and meet the demand of a growing global population. Direct-seeded rice (DSR) has emerged as a sustainable alternative to traditional puddled transplanted rice, primarily due to its reduced input requirements, particularly water, as it eliminates the need for continuous field submergence. Simultaneously, it reduces labour requirement as it eliminates the need for a nursery. DSR offers significant advantages, including reduced water use (up to 50 %), lower greenhouse gas emissions, decreased labour dependency, improved soil health and enhanced economic returns. However, its widespread adoption is hindered by several challenges such as poor seedling establishment, high weed pressure, lodging susceptibility and nematode infestations. Recent advances in next-generation breeding strategies, including genome-wide association studies, gene editing, genomic selection and haplotype-based breeding, are increasingly being applied to address these challenges and develop rice varieties for DSR systems. Essential adaptive traits for successful DSR establishment include anaerobic germination potential, early seedling vigour, herbicide tolerance, strong root architecture and lodging resistance. By highlighting the critical role of these traits in DSR adaptation, this review underscores their potential impact and offers insights to advance DSR practices, while outlining the prerequisites for its successful cultivation.

Keywords: anaerobic germination; direct seeded rice; early seedling vigour; herbicide tolerance

Introduction

India, producing 27 % of global rice, cultivates the crop on 51 Mh with an output of 147 MMT (USDA, 2024). According to the World Health Organisation (WHO), India's population is projected to reach 1.67 billion by 2050, necessitating a substantial increase in rice production to meet rising food demands. However, the total area of arable land is shrinking due to urbanization, industrialization and climate change. Global rice demand is expected to reach 584 Mt by 2050, even as 5 Mh of rice land are predicted to disappear worldwide (1). This dual challenge of increasing demand and declining land availability calls for urgent measures to boost productivity. If India's rice area declines by 15 %, yields must reach 2.62 t/ha in order to meet demand (2). Achieving this target will require sustainable and economically viable strategies that enhance productivity without compromising environmental health.

Among the four rice ecosystems, irrigated rice remains the most dominant in terms of both cultivated area and production. Globally, the irrigated rice ecosystem accounts for 55 % of the total rice-growing area and contributes approximately 75 % of rice production. Looking ahead, agricultural water

demand is projected to rise by 20 % by 2050, while India, a major rice producer, holds only 4 % of the world's freshwater resources (India-WRIS, 2018) (3). Therefore, it is essential to adopt water-efficient cultivation methods that not only minimize water use but also enhance water productivity and improve net returns. Yet, rice productivity is increasingly threatened by declining groundwater levels, natural resource depletion, labour shortages, rising energy and input costs and the escalating effects of climate change (4).

Climate change is further driving the shift away from traditional rice cultivation, largely due to the significant greenhouse gas (GHG) emissions associated with waterlogged transplanted paddy fields. The United Nations Environment Programme reported a 1.2 % rise in global GHG emissions from 2021 to 2022. Meanwhile, the World Meteorological Organization (2023) recorded alarming concentrations of CO₂ (420 ppm), methane (1934 ppb) and nitrous oxide (336.9 ppb). In Punjab, transplanted rice has been reported to have a global warming potential of 2 to 4.6 t CO₂ eq/ha (5).

The benefits of decreasing the water footprint (35 %- 57 %) along with lowering labour use, improving the benefit-cost ratio

and decreasing methane emissions have led rice farmers to shift their transplanted puddled rice (TPR) to DSR (6). DSR cultivation involves sowing seeds directly in the main field, thus eliminating the requirement for a nursery. In ancient days, direct seeding of rice was a common practice in Asia, predating the adoption of transplanting (7). In India, DSR occupies nearly 50 % of rice-growing areas, under rainfed conditions (8). DSR cultivation is currently being practiced in several Indian states like Punjab, Haryana, Uttar Pradesh, Andhra Pradesh, Telangana, Madhya Pradesh (9, 10, 11). The rainfed rice-growing areas in India, the eastern part of India (Orissa, Assam, West Bengal, Bihar, Chhattisgarh, Uttar Pradesh, Jharkhand and Madhya Pradesh) contributes about 70 % wherein rainfed lowland accounts for 27 % of the total area and rainfed upland accounts for 11 % of the total area (12). This system is increasingly being considered as a sustainable alternative to conventional puddled transplanted cultivation, as it enhances productivity under water-scarce and labour-limited conditions while offering a more environmentally friendly approach.

Direct seeded rice (DSR) cultivation

DSR refers to the method of establishing a rice crop by sowing seeds directly into the field, by passing the traditional practice of transplanting seedlings from a nursery (13). The introduction of high-yielding, fertilizer-responsive rice varieties during the Green Revolution led to significant changes to rice cultivation practices in India. These newly developed varieties performed more effectively under puddled transplanted rice (PTR) conditions, making PTR the preferred method of cultivation. However, the growing threats of natural resource depletion, shrinking arable lands, declining water table levels, mounting labour shortages, increasing input prices and energy constraints hamper rice production. In response to these issues, many farmers are transitioning from traditional PTR to DSR.

DSR has been practiced in several Asian countries like Cambodia, Vietnam, Malaysia, Thailand, Sri Lanka and the Philippines. In India, DSR has been practiced in areas with uneven rainfall distribution and soil moisture limitations, such as Tamil Nadu, Karnataka, Chhattisgarh, Jharkhand, parts of Bihar, Odisha and eastern Uttar Pradesh (14).

DSR cultivation can be classified into three main types: dry DSR, wet DSR and water-seeding (Fig. 1). In Dry DSR, seeds are broadcasted in dry field, whereas in wet DSR, pre-germinated seeds are sown into puddled soil, which may be aerobic or anaerobic (15). Water seeding, on the other hand, involves sowing dry or pre-germinated seeds into standing water.

Both dry and wet seeding methods are commonly practiced by rainfed rice farmers in lowland areas and are gradually gaining popularity in irrigated ecosystems as well, primarily due to their lower labour and time requirements compared to traditional transplanting methods (16). Among these, dry DSR offers the highest water-use efficiency and facilitates mechanization (17). The selection of the direct-seeded system type depends on several environmental and socioeconomic factors (18). In a study conducted in Kamal district of Haryana, it was found that direct seeding has saved the use of human labour, machine labour and irrigation water by 13.16 %, 41.34 % and 11.88 % respectively (10). Similarly, direct seeding of dry and sprouted seeds has reduced the cost of production by 19.94 %, compared to PTR (19). Although yield outcomes between DSR and PTR vary depending on environment and cultivar, studies have shown that under stress during vegetative and reproductive stage, yield losses were higher in PTR (27 % and 43 %) than in DSR (20 % and 31 %) (20).

Direct seeding can be done in both conventionally tilled and zero-tilled systems. Zero tillage offers additional benefits such as reduced production costs, lower fuel consumptions and improved soil structure. However for maximizing the potential of DSR, cultivars specifically bred for no-till conditions are required, coupled with optimized nutrient, water and weed management practices. Addressing these gaps will be essential for large-scale adoption and long-term sustainability of DSR systems.

Advantages of direct-seeded rice cultivation

DSR is an emerging cultivation system that offers a sustainable and cost-effective alternative to traditional rice transplanting. The key advantages of DSR cultivation are highlighted in Fig. 2.

Resource friendly: DSR has recently been promoted as a resource-friendly cultivation method by various national and international agencies advocating climate-resilient practices and policies. Under changing climatic scenario, water scarcity has

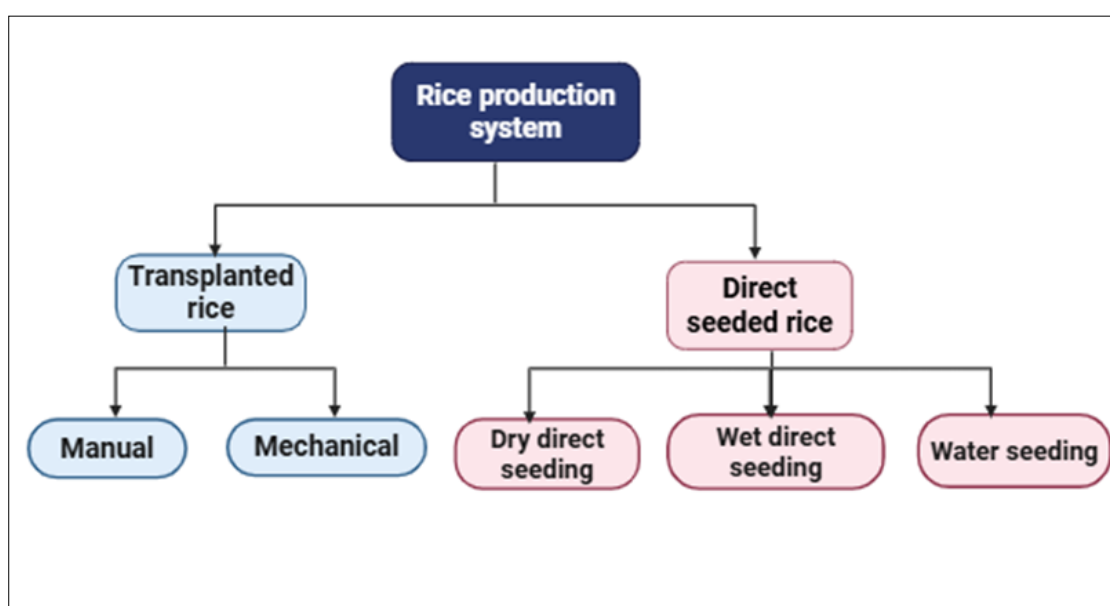


Fig. 1. Classification of rice cultivation system.

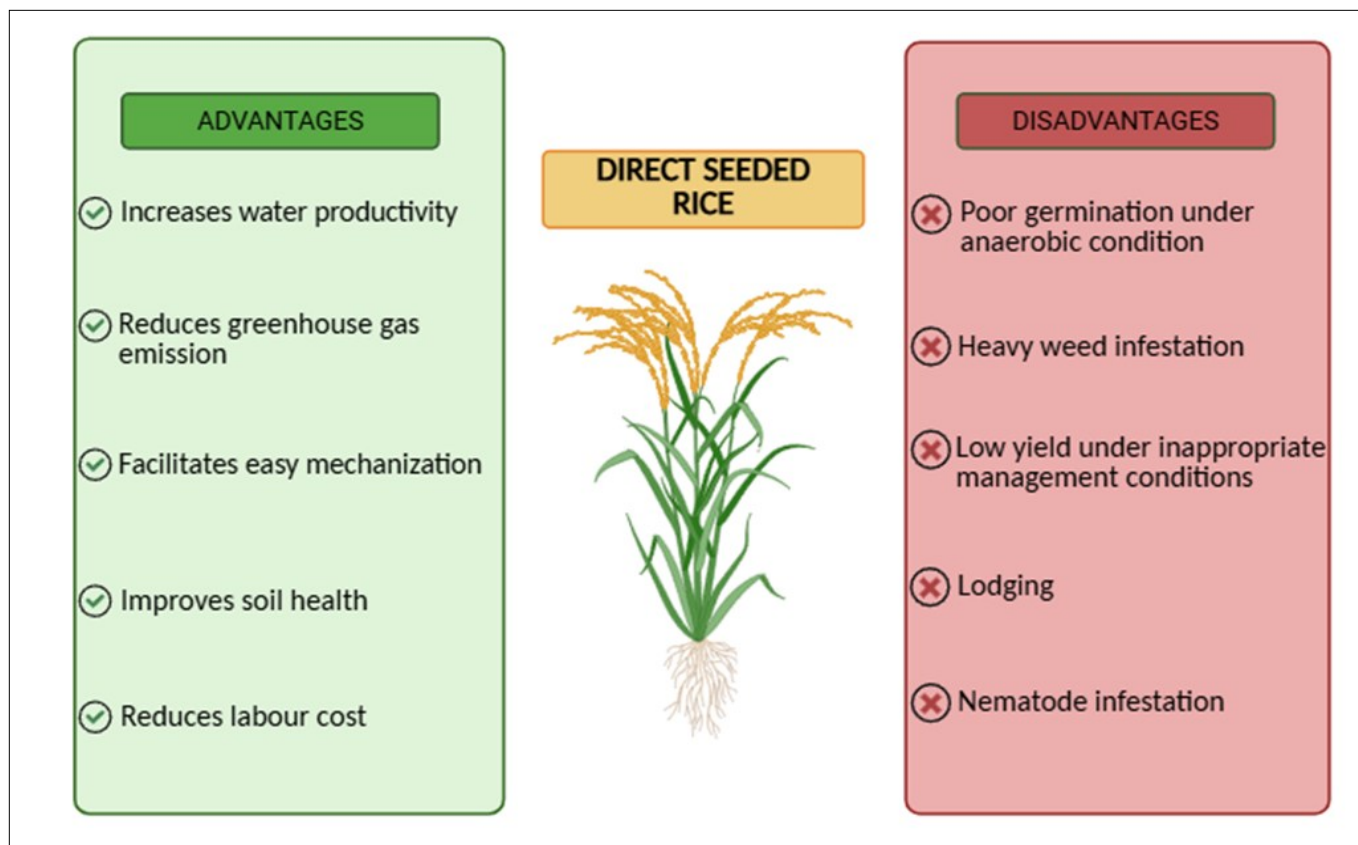


Fig. 2. Advantages and disadvantages of direct seeded rice system.

become one of the key drivers prompting a shift from traditional transplanting to direct seeding. Land preparation in transplanted rice is one of the most water-intensive steps. In contrast, DSR reduces water requirements during land preparation by about 29 %, with overall water savings reported to range between 10 % to 50 %, depending on location and management practices (21-23). Comparative studies have shown that dry DSR systems require the least irrigation water and achieve the highest water productivity among different rice production systems (22).

In addition to water savings, the adoption of DSR significantly reduces labour costs, thereby making rice cultivation more economically viable, especially in regions facing water and labor shortages (23). Labour savings under DSR have been reported to range from 11 % to 75 % compared to PTR, with some studies citing reduction of up to 46 % in labour costs (23-25). Furthermore, cropping systems based on DSR have shown higher profitability, with labour savings of 22 %-31 % over PTR (24). Studies have reported labor reductions ranging from 11 % to 75 % under DSR compared to PTR (25).

Environment-friendly: Under water-logged anaerobic conditions, the decomposition of organic matter results in the release of greenhouse gases like methane, carbon dioxide and nitrous oxide, thus leading to global warming (26). About 30 % of the total methane and 11 % of total nitrous oxide released through agricultural activities is from rice fields (26). In DSR, since water is not stagnant, anaerobic decomposition is minimized, leading to a reduction in greenhouse gas emissions. DSR has been reported to reduce methane gas emissions by approximately 85.6 % to 96.8 % (27). An InfoRCT simulation model conducted in Jalandhar showed that methane emissions from DSR (0 to 0.1 kg/ha/day) were significantly lower than those from transplanted rice (0.2 to 0.8 kg/ha/day). Converting all rice cultivation in Punjab to DSR could

potentially reduce the regions' global warming potential by approximately 33 % (5). However, this is not an easy task, as it will take time to persuade farmers of the benefits of direct seeding and encourage them to transition from their traditional cultivation methods.

Early maturation of crop: Direct seeding can facilitate early maturation through its faster establishment in main field. Moreover, DSR shortens the cropping cycle by eliminating transplanting shock, thus saving valuable time. The crops under DSR mature 7 to 10 days earlier than those grown using traditional methods (28). Similarly, direct seeding of dry and sprouted seeds matured about one week earlier than transplanted crops (19). Its earlier maturation compared to PTR makes DSR a more suitable choice for diverse cropping systems (24). In transplanted rice, when seedlings are uprooted from the nursery, fine roots are damaged, which temporarily reduces water and nutrient absorption (29). The plant must then regenerate its root system, causing a lag in growth. By shortening the growth duration, DSR enables crops to escape terminal drought and allows better integration into intensive cropping systems, ultimately improving overall farm productivity (30).

Improving soil health: The conventional method of transplanting rice involves puddling, which means ploughing the field under submerged conditions several times so as to get the ideal soil condition for transplanting. Although puddling has its advantages, in the long run this can have a significant negative impact on soil health. A study evaluated the effects of different puddling intensities, like no puddling and puddling with four and eight passes of a power tiller (31). The study found that the mean weight diameter (MWD) of soil aggregates decreased by 22 % and 46 % in the second and third treatments after the first and second years, respectively. A lower MWD reflects weaker soil structure and

higher susceptibility to erosion, as greater MWD indicates better aggregation and porosity. In contrast, aggregate stability remained nearly unchanged in non-puddled soil. Furthermore, compared to conventional puddling, non-puddled rice establishment combined with increased crop residue retention improved soil quality, raising soil organic carbon by 79 % and total nitrogen by 62 % (32). Alternative rice establishment methods, such as DSR, the System of Rice Intensification (SRI) and non-puddled transplanting, have been shown to improve the soils' physical, chemical, microbial and faunal properties (33).

Mechanization: Mechanization helps address labour shortages by reducing field labour requirements. Beginning with sowing, the use of a drum seeder or direct seeding machine can reduce seed rates by 61 %-83 % compared to traditional broadcasting methods in transplanted rice. Line seeding not only lowers seed use but also ensures uniform seedling establishment and improves resource-use efficiency (34). Furthermore, deep placement using a mechanical hill DSR machine enhanced yield, nitrogen use efficiency and the activity of catalase and peroxidase enzymes in plants (35). Catalase and peroxidase enzymes are key indicators of stress tolerance and metabolic activity, contributing to improved growth under field conditions. Mechanization is more feasible in DSR systems than in puddled transplanted rice.

Beyond efficiency, mechanization in DSR helps in weed management. Weed infestation under drill seeding was 26 %-36 % lower than in broadcasting and 16 %-24 % lower than in manual line seeding at 30 and 60 days after emergence respectively (36). Drill seeding also proved more profitable, yielding a net income of US\$685 per hr, primarily due to better plant stand establishment and reduced weed pressure, which led to higher yields.

Crop management and economics: Direct seeding of rice reduces overall cultivation costs by lowering expenses on irrigation, labour and machinery, resulting in a higher benefit-cost ratio of 2.92 compared to 2.61 for transplanted rice (10). DSR has been shown to reduce labour costs by 6.62 % compared to transplanted rice (10). However, successful adoption of DSR requires farmers to have adequate knowledge of crop management practices. Direct seeding has been estimated to cost approximately ₹1260 per acre i.e. only one-third of the transplanting cost (₹3787 per acre) (11). Among direct seeding methods, sowing sprouted seeds resulted in higher benefit-cost ratio of 1.49:1 (19).

DSR saved about Rs 2400 per acre compared to transplanted rice, despite incurring higher costs for weedicides and micronutrients (around ₹730 per acre) (37). Since net returns remain higher, these additional expenses can be managed by farmers. Moreover, the extent of amount saved depends on the crop management practices adopted during cultivation. Therefore, adherence to standardized practices is essential to achieve consistent results; otherwise, net returns may vary. Although yields under DSR are sometimes slightly lower than under transplanted rice, the overall reduction in cultivation expenditure leads to higher net returns, making DSR an economically advantageous system.

Challenges in practising DSR

While DSR offers several benefits, it also presents certain challenges that must be considered, as depicted in Fig. 2. These challenges span biological, agronomic and environmental domains and have significant implications for productivity and sustainability.

Poor seedling establishment

Low germination rates and uneven plant populations are critical constraints limiting growth and development in DSR. Successful crop establishment requires the selection of seeds with high germination potential and rapid seedling vigour (38). Rather than relying solely on increasing seed rates to enhance crop establishment, which can lead to nitrogen deficiency, lodging, increased pest susceptibility and ultimately reduced grain yield, emphasis should be placed on early seedling vigour as a key trait in breeding cultivars suitable for direct seeding (39). Enhanced seedling vigour also improves the crops' competitive ability against weeds, making it a useful trait to distinguish between cultivars that are either tolerant or susceptible to weed pressure (40, 41). A comprehensive focus on traits associated with seedling vigour is therefore essential to ensure reliable establishment and sustained crop performance. Integrating these traits into breeding programmes will be key for ensuring reliable establishment under diverse field conditions.

Weed infestation

Weeds are one of the major biotic constraints limiting productivity in direct seeded rice cultivation (42). Unlike transplanted rice, where standing water suppresses weed growth, the aerobic conditions of DSR, along with intermittent irrigation and the absence of water stagnation, create favourable conditions for weed emergence (13). Around 350 weed species infest rice fields and the shift from puddled transplanted rice to DSR has significantly altered weed composition and increased weed pressure (24, 43). Common weeds in DSR include *Echinochloa crus-galli*, *Leptochloa chinensis*, *Cyperus iria*, *Cyperus difformis*, *Eclipta prostrata* and *Ludwigia octovalvis* (43). A study reported the yield losses of up to 99 % in DSR due to weed infestation, highlighting the need for integrated weed management strategies (44). Similarly, proliferation of weeds can lead to yield losses exceeding 20 % and in severe cases, may result in complete crop failure if not properly managed (45). Therefore, an effective weed management is crucial for the success of DSR systems (46). Although hand weeding remains the most effective method for controlling weeds and improving yields, it is labour-intensive, leading farmers to prefer chemical herbicides. However, improper herbicide use can lead to herbicide resistance, degrade soil health and harm the rice crop (13, 47). Consequently, research is underway to develop herbicide-tolerant rice cultivars to enable more sustainable weed control in DSR systems. Effective weed management in DSR requires a multi-pronged approach, combining timely land preparation, competitive cultivars, water management and selective herbicide use.

Nematode infestation

In DSR cultivation, certain soil-borne pathogens, particularly nematodes, are actively prevalent. The root-knot nematode *Meloidogyne graminicola* is commonly found in the rice root zone, thereby limiting yield (48). Its abundance is influenced by rainfall, agroecosystem and temperature. They found that *M. graminicola* infestation was more severe in dry direct-seeded and rainfed upland fields compared to lowland systems, with the highest populations observed in dry aerobic fields in China, where low soil moisture favours nematode proliferation. Additionally, eggs are laid inside roots during flooding and outside roots under drier conditions, underscoring the need for targeted field management (49). Inoculating rice with arbuscular mycorrhizal fungi viz., *Funneliformis mosseae*, *Rhizophagus fasciculatus* and *R. intraradices*, either alone

or in combination, activates molecular and biochemical defense pathways, enhancing enzyme activities associated with plant resistance to *M. graminicola* (50). Such symbiotic associations could be incorporated into seed or soil inoculation programs to reduce nematode damage in DSR fields (51).

Lodging

Lodging is another major constraint in direct-seeded rice cultivation, leading to significant yield losses. It is influenced by both morphological traits and weather conditions (52). Stem lodging and root lodging are the different types of lodging in cereals, out of which root lodging is more common in dry direct-seeded rice due to its shallow root system (53). Morphological traits such as culm thickness and diameter play a critical role in lodging resistance (54). To enhance lodging resistance and improve yield in DSR, identifying quantitative trait loci (QTLs) linked to culm traits is essential (55).

Comparison between DSR and system of rice intensification (SRI)

DSR and SRI are two alternative cultivation methods developed to reduce the resource intensiveness of conventional puddled rice cultivation. DSR reduces water and labour requirements as well as helps in faster crop establishment. However, it poses some problems like poor crop stand, higher weed infestation and low nutrient efficiency (23, 56). In contrast, SRI involves transplanting young seedlings at wider spacing under an intermittent irrigation system combined with mechanical weeding. SRI is known to enhance tillering, root growth and grain yield but requires more labour and skilled management (57, 58). Thus, while both systems aim to promote sustainable rice production, DSR is more suited to areas with acute water and labour scarcity, whereas SRI primarily focuses on yield enhancement through resource-conserving agronomic practices.

A field trial was conducted to compare wet DSR, flooded transplanted rice (FTR) and SRI using 15 rice varieties. Wet DSR showed a reduction in many traits like tiller number tiller number (-26.8 %), panicle length (-7.5 %), panicle weight (-12.7 %), spikelets per panicle (-16.1 %), thousand-grain weight (-3.2 %),

biological yield (-3.8 %) and grain yield (-25.0 %) compared with FTR. On the other hand, SRI enhanced these traits, with increases in tillers per plant (+19.0 %), panicle length (+1.0 %), panicle weight (+8.3 %), spikelets per panicle (+8.4 %), thousand-grain weight (+1.4 %), biological yield (+13.6 %) and grain yield (+16.2%) relative to FTR. Among the varieties tested, CSR 30 showed the least reduction under wet DSR, whereas Pusa Basmati 1121 exhibited the maximum improvement under SRI. Regression analysis indicated that tiller number, biological yield, panicle length, days to maturity and thousand-grain weight were the primary contributors to grain yield variation under wet DSR, whereas tiller number, biological yield, days to maturity and thousand-grain weight were more influential under SRI (59). Thus, this study signifies that varietal selection, coupled with the appropriate establishment method, can significantly improve rice productivity under diverse conditions of water and labour scarcity.

Adaptation traits for next-gen direct seeding

The challenges mentioned must be overcome before DSR can be widely adopted as a climate-resilient rice cultivation method. Currently, varieties developed for puddled transplanted systems are also used in direct seeding, which limits the full exploitation of yield potential under DSR conditions. This underscores the need to develop varieties specifically tailored for DSR conditions. DSR-adapted varieties should possess traits such as early vigour, anaerobic germination tolerance, the ability to germinate from deeper soil layers and resilience to unfavourable conditions (Fig. 3) (17). Traditional landraces represent a valuable reservoir of desirable alleles for key agronomic traits. Although generally less productive, they exhibit strong weed-suppressing ability through early vigour and possess adaptive growth characteristics well-suited to direct-seeded conditions. The success of any crop breeding program relies on understanding existing genetic variability to enhance selection efficiency. However, only a small fraction of traditional landraces has been utilized in breeding programs. Therefore, assessing the genetic diversity of traditional rice cultivars is crucial to identify donor parents and key genes for traits like early seedling vigour and anaerobic germination tolerance, which are essential for developing DSR-adapted varieties.

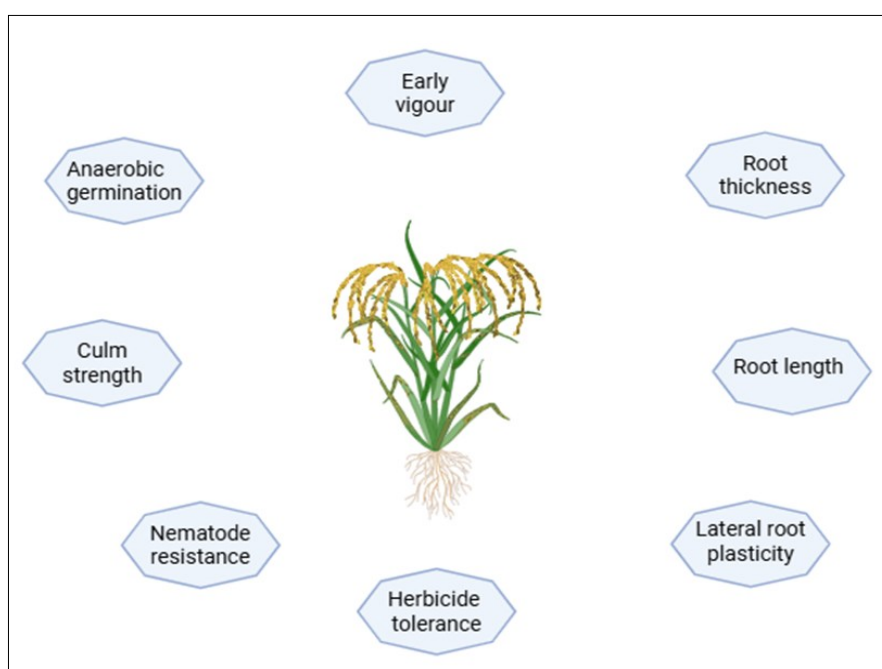


Fig. 3. Adaptive traits for Next-Gen direct seeding.

Anaerobic germination potential

In direct-seeded conditions, improper field levelling can lead to water stagnation in certain patches, creating anaerobic conditions. To ensure successful germination, seeds must tolerate temporary flooding stress. Germination under anaerobic conditions largely depends on the rate of coleoptile elongation towards the water surface, which varies among accessions (60). Anaerobic stress often results in poor and uneven crop establishment due to limited germination (61). Under flooded conditions, shoot growth initiates earlier and progresses more rapidly than root growth, despite reduced ATP production under hypoxia, which can hamper germination (62). Rice seeds possess a unique ability to germinate under low-oxygen conditions by degrading stored starch to produce ATP, thereby supporting coleoptile growth (63).

Moreover, the enzyme Calcineurin B-like interacting protein kinase (CIPK15) detects oxygen deficiency and in coordination with SnRK1A, regulates sugar metabolism during submergence, sustaining ATP production under stress (64). Tolerant genotypes degrade stored starch to generate ATP for germination under flooded conditions, resulting in decreased starch and increased soluble sugar content after sowing (62). Accessions with high germination percentages also showed elevated α -amylase activity and suggested that higher gibberellic acid levels in tolerant genotypes may aid coleoptile elongation under submerged conditions (65).

Similarly, shoot elongation is a characteristic trait of genotypes tolerant to anaerobic germination, as seedlings attempt to reach above the water surface for better aeration (61). Landraces such as *Vellai Kavuni*, *Varappu Kudaichan*, *Norungan* and *Karuppu Kavuni* have demonstrated strong anaerobic germination capacity, with over 90 % germination and high dry matter accumulation during phenotypic screening (66). These landraces hold significant potential for use in marker-assisted breeding programs to incorporate this valuable trait using molecular markers.

Early seedling vigour

Early seedling vigour (ESV) is a critical determinant of successful crop establishment in DSR, as it ensures rapid and uniform emergence under variable field conditions. ESV encompasses both seed vigour-the inherent quality and viability of seeds-and seedling vigour, which reflects the plants' growth potential during the early developmental stages. It ensures consistent germination and seedling growth, facilitating successful crop establishment across diverse environmental conditions (67). ESV denotes the plants' growth during both the seedling and post-seedling stages. Thus, breeding for enhanced seedling vigour is a major breeding target in DSR, as it promotes vigorous growth, better seedling establishment and ultimately contributes to higher yield and improved resilience to adverse climatic conditions (68).

Therefore, identifying promising donor lines with strong ESV traits is imperative for breeding lowland rice cultivars, as it enhances weed-competitive ability. Traits such as seed dormancy, germination rate, root and shoot dry weight and the activities of enzymes like amylase along with levels of reducing sugars, are closely related to seed vigour, contributing to uniform seedling growth by ensuring adequate energy supply (6, 67). So, it is essential to focus on these associated traits also to get better seedling vigour.

Herbicide tolerance

The development of herbicide-tolerant rice varieties offers a sustainable and environmentally friendly solution for effective weed control. Rice varieties tolerant to three major herbicides viz. glyphosate (Roundup Ready), imidazolinone (Clearfield rice CL121 and CL141 (T)), glufosinate (Liberty Link rice LL Rice 601) have been developed (69, 70, 71). Among these, glyphosate and glufosinate tolerance was achieved through transgenic breeding, while imidazolinone tolerance was developed through chemical mutagenesis (72). Each herbicide operates through a distinct mode of action. Glyphosate inhibits the enzyme 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) by competing with its natural substrate. Thus, a glyphosate-resistant EPSPS gene from a bacterium with reduced glyphosate affinity was introduced into rice thereby conferring herbicide tolerance (73). Glufosinate on the other hand, contains phosphinothricin, which inhibits glutamine synthetase, leading to plant death (72). The *bar* and *pat* genes from *Streptomyces* encode phosphinothricin acetyltransferase and their introduction into rice plants confers glufosinate tolerance (74).

Although herbicide tolerant varieties of many crops have been developed, these have not been commercialized to a great extent. This is largely due to the high costs of obtaining regulatory clearance and international trade concerns associated with genetically modified (GM) crops (75).

Given the high regulatory costs and market concerns surrounding GM crops, non-GM herbicide-tolerant rice offers a more acceptable pathway for adoption, particularly in regions with strict biosafety regulations. A significant breakthrough in non-GM herbicide tolerance was achieved with the development of the HTM-N22 mutant (later named *Robin mutant*), derived by chemically mutating the upland rice variety Nagina 22 using ethyl methanesulfonate. The mutant exhibited tolerance to Imazethapyr due to a mutation in the acetohydroxy acid synthase (AHAS) gene (76). This Robin mutant was subsequently used to develop various herbicide-tolerant rice varieties. In 2021, India's first non-GM herbicide-tolerant basmati varieties, Pusa Basmati 1979 and Pusa Basmati 1985 were released by IARI. Similarly, CR Dhan 807 was the first non-GM, non-basmati herbicide-tolerant variety released in India (77).

Herbicide-tolerant rice helps not only for sustainable weed management but also for increasing grain yield and reducing labour costs associated with manual weeding.

Lodging resistance

Lodging resistance is essential for the success of DSR systems, which are more prone to lodging due to faster early growth, weaker stems and shallow roots. Resistance to lodging is associated with culm strength, which is the mechanical strength of rice stem (78). Identification of genes conferring lodging resistance through QTL analysis and positional cloning has proven effective in enhancing lodging resistance in rice. Habataki, an improved *indica* rice variety, can be used as a donor parent to develop lodging resistant varieties as it possesses very strong culms (54). Increased culm thickness and diameter are the key targets for improving lodging resistance in rice (53). They crossed a *smos1* (small organ size 1) mutant characterized by low tillers, lesser grain yield and strong lodging resistance with a cultivar ST-4 having more tillers and good yield. From this progeny, a candidate named lodging-resistant candidate 1 (LRC1) was selected, which combined high grain

weight per panicle with lodging resistance inherited from *smos1*. Foliar application of paclobutrazol at panicle initiation in rice cultivars MR219 and MR84 reduced plant height by inhibiting gibberellin production, which shortened internode length and blocked cell elongation (79). Despite the reduction in height, culm diameter increased, enhancing bending resistance and effectively preventing lodging. This highlights the importance of using plant growth regulators at appropriate doses, along with fertilizers and crop protection chemicals, to optimize rice growth and lodging resistance.

Root architecture

Root system architecture (RSA) traits play a crucial role in improving productivity under DSR cultivation, as they influence water and nutrient uptake, anchorage and stress resilience (80). Root plasticity is crucial for efficient water uptake and enhanced shoot dry matter production, especially under rainfed lowland conditions (81). The plasticity of RSA enhances the adaptability of rice to diverse environmental conditions by enabling efficient resource acquisition and stress tolerance. Plasticity of root architecture was positively correlated to grain yield stability (82). Root activity plays a key role in dry matter accumulation and translocation during the growing season, directly affecting grain yield (83). Therefore, understanding RSA and plasticity is essential for optimizing rice cultivation, particularly under changing environmental conditions and increasing sustainability demands.

Next-Gen breeding strategies for DSR

Traditional agricultural practices have gradually reduced crop genetic variability, thereby limiting the potential for developing novel plant varieties through conventional breeding (84). Now a days, plant breeders leverage advanced tools such as high-throughput phenotyping, genome editing and speed breeding to accelerate crop improvement (84). These modern breeding tools enable the precise identification of desirable genes, accelerating the development of improved crop varieties. However, the adoption of DSR and water-saving practices like alternate wetting and drying introduce new challenges that modern rice breeding must address.

Marker assisted breeding

Modern breeding tools enable the identification of plants carrying desirable genes, thereby accelerating crop improvement. Marker-assisted selection (MAS) is a key technique that facilitates genetic enhancement by using markers linked to specific chromosome segments for the selection of superior plants (85). A QTL hotspot on chromosome 12 has been identified for both culm strength and grain number, making it a promising target for the simultaneous improvement of these traits (86). Similarly, the *SCM2* QTL for culm strength, exhibited pleiotropic effects by increasing spikelet number in near-isogenic lines (54). Later, it was found to be identical to the *APO1* gene, which also regulates panicle structure.

MAS enables precise targeting of QTLs for desirable traits, thereby accelerating the development of new varieties (Table 1).

For instance, marker-assisted backcrossing (MABC) was employed to transfer anaerobic germination tolerance from the indica landrace *Kho* to the japonica cultivar *Dongan* (98). MAS targeting tolerant alleles of AG1 and AG2 using SSR markers RM24161, RM478 and the InDel marker TPP_G4 enhanced

selection efficiency and identified four lines with improved anaerobic germination.

MAS also facilitates the pyramiding of multiple QTLs from diverse donor sources, accelerating the development of improved crop varieties with combined desirable traits. For example, pyramided drought tolerance QTLs (*qDTY1.1*, *qDTY2.1*, *qDTY3.1*) with the submergence tolerance QTL *Sub1* into the variety *Swarna* resulted in significantly improved yield and stress resilience under DSR conditions (99).

Genome-wide association studies

Genome-wide association studies (GWAS) are powerful tools for uncovering the genetic basis of complex traits like seedling establishment, root morphology and grain yield. The aim was to identify significant associations and QTLs for use in marker-assisted breeding to develop rice varieties adapted to DSR systems. GWAS was conducted on a Multi-parent Advanced Generation Inter-Cross (MAGIC) population, to identify marker-trait associations relevant to dry direct-seeded rice cultivation (100). They identified 37 significant associations for 20 key traits, including root architecture, nutrient uptake, yield components, lodging resistance and plant morphology. Seven progenies with desirable trait combinations were identified as promising candidates for genome-assisted breeding to develop new DSR-adapted rice varieties. Another study was conducted on 421 rice cultivars to test the resistance to three herbicides glufosinate, glyphosate and mesotrione (101). Two major QTLs *RGLu6* and *RGLu8*, conferring resistance to glufosinate and glyphosate, with resistance alleles mainly found in European *japonica* varieties. Thus, GWAS has emerged as a promising approach to develop desirable varieties.

Gene editing

The discovery of the CRISPR/ Cas system marked a major breakthrough in gene editing, providing a powerful tool for modern crop improvement. Previous study utilized CRISPR/Cas9 to edit the *OsALS* gene (acetolactate synthase) in the high-yielding Chinese rice cultivar Nangeng 9108, creating a new allele, G628W, through a G-T transversion (102). This allele conferred tolerance to the herbicides imazethapyr and imazapic and the edited mutants were successfully validated for herbicide tolerance through phenotypic screening at various herbicide doses. CRISPR/Cas9 mediated gene editing was done to domesticate weedy rice for direct-seeded cultivation by targeting the *Rc* gene responsible for red pericarp, a trait that negatively affects grain quality (103). Editing the gene disrupted its bHLH domain, resulting in three white-pericarp mutants. Interestingly, these edited lines also showed improved drought tolerance during early emergence. This may be due to the pleiotropic role of the *Rc* gene in promoting abscisic acid expression, which induces seed dormancy (104).

Disruption of this gene may enhance germination and contribute to drought resilience. Thus, it was concluded that eliminating undesirable traits through gene editing can help convert weedy rice, a major threat in DSR systems into a beneficial cultivar (100, 103). These studies highlight the potential of gene editing as an effective tool for developing tailored varieties suitable for direct seeding. However, further research is required and greater emphasis should be placed on advancing this approach.

Table 1. QTLs identified for adaptation traits for Next-Gen direct seeding

Sl. No.	Trait	Parents	Mapping population	QTL	Chromosome	Marker	PVE (%)	Reference
1	Anaerobic germination	IR64/ Khaiyan	BC ₂ F ₂	<i>qAG-1</i>	1	RM 312	25.23	(87)
				<i>qAG-2</i>	2	RM341	14.5	
				<i>qAG-11</i>	11	RM206	21.1	
				<i>qAG-12</i>	12	RM28759	29.24	
				<i>qAG2</i>	2	RM263-RM5378	13.4	
2	Anaerobic germination	IR42/Ma-Zhan Red	F ₂ -F ₃	<i>qAG5</i>	5	RM5361	8.8	(88)
				<i>qAG6</i>	6	RM204-RM402	1.5	
				<i>qAG7.1</i>	7	RM3583-RM21427	23.5	
				<i>qAG7.2</i>	7	RM7338-RM346	19	
				<i>qAG7.3</i>	7	RM21803-RM234	9.6	
			F ₂	<i>qAG9</i>	9	RM553-RM3808	-	
				<i>qAG12</i>	12	RM313-RM28766	8.2	
				<i>qAG2.1</i>	2	id2001831-id2003094	-	
				<i>qAG2.2</i>	2	id2006621-id2007526	9.94	
				<i>qAG3</i>	3	id3007932-id3010875	18.32	
3	Anaerobic germination	IR64/ Nanhi	F ₂	<i>qAG7</i>	7	wd7000465-id7002784	13.06	(89)
				<i>qAG11</i>	11	id11009201-id11010245	18.21	
				<i>qEV_{3.1}</i>	3	id3010740	7.2	
				<i>qEV_{3.2}</i>	3	id3005879	13.1	
				<i>qEV_{4.1}</i>	4	id4011683	12.1	
				<i>qEV_{5.1}</i>	5	wd5002636	7.4	
				<i>qEV_{5.2}</i>	5	id5003638	6.6	
				<i>qEV_{6.1}</i>	6	id6011613	10.6	
				<i>qCS_{1.1}</i>	1	id1003559	14	
				<i>qCS_{2.1}</i>	2	id2007818	12	
4	Early vigour	Swarna/ Moroberekan	BC ₃ F ₄	<i>qCS_{2.2}</i>	2	id2006621	27	(6)
				<i>qCS_{2.3}</i>	2	id2008112	31	
				<i>qCS_{6.1}</i>	6	id6001960	11	
				<i>qCS_{6.2}</i>	6	id6010515	8	
				<i>qCD_{1.1}</i>	1	id2007818	13	
				<i>qCD_{2.1}</i>	2	id2007818	13	
5	Culm strength	Swarna/ Moroberekan	BC ₃ F ₄	<i>qCD_{7.1}</i>	7	id7001246	12	(52)
				<i>qRG_{4.1}</i>	4	id4004802	6.6	
				<i>qRG_{8.1}</i>	8	ud8000289	5.2	
				<i>qAG3</i>	3	id3003215	-	
				<i>qAG7.1</i>	7	wd7000465	12.5	
				<i>qAG7.2</i>	7	d7003072	13.5	
6	Culm diameter	Swarna/ Moroberekan	BC ₃ F ₄	<i>qAG7.3</i>	7	id7004429	12.6	(91)
				<i>qAG1</i>	1	1.25043823- 863795	13.44	
				<i>qAG3</i>	3	2495249-2497338	6.71	
				<i>qAG11</i>	11	10922039- 11.3839501	14.52	
				<i>qAG1-2</i>	1	RM272-RM490	13	
7	Root galling	IR64/ IR78877-208-B-1-2	RILs	<i>qAG6-2</i>	6	RM508-RM510	15	(92)
				<i>qAG7-4</i>	7	RM481-RM21427	18	
				<i>qAG10-1</i>	10	RM258-RM304	15	
				<i>qAG5</i>	5	S05_9596301	5.4	
				<i>qAG6</i>	6	S06_11109090	5	
8	Anaerobic germination	IR64/Kharsu 80A	F ₂	<i>qAG7</i>	7	S07_7547815	15.1	(94)
				<i>qAG9</i>	9	S09_12277535	29.4	
				<i>qAGP1</i>	1	Bin38	66	
				<i>qAGP3</i>	3	Bin346	64	
				<i>qCV1-1</i>	1	Bin117-Bin118	0.55	
9	Anaerobic germination potential	93-11/ W2014	ILs	<i>qCV1-2</i>	1	Bin329-Bin330	1.62	(96)
				<i>qCV8-2</i>	8	Bin8412-Bin8413	0.53	
				<i>qCL4-2</i>	4	Bin3788-Bin3789	5.59	
10	Coleoptile volume	TD70/ Kasalath	RILs	<i>qCSA4-2</i>	4	Bin4035-Bin4036	3.31	(96)
				<i>qCSA6</i>	6	Bin6167-Bin6168	2.24	
				<i>qCSA8</i>	8	Bin7941-Bin7942	2.02	
11	Coleoptile length	TD70/ Kasalath	RILs	<i>qSL3</i>	3	RM570	8.97	(97)
				<i>qRL7</i>	7	RM1132	6.51	
12	Coleoptile surface area	TD70/ Kasalath	RILs					(96)
13	Shoot length	Xiushui134/Yangdao6	CSSLs					(97)
14	Root length	Xiushui134/Yangdao6	CSSLs					(97)

Rice varieties tailored for direct-seeded farming

To ensure the long-term sustainability and productivity of DSR cultivation, it is crucial to develop varieties specifically tailored for DSR conditions. To keep up the pace with the changing scenario, ICAR-National Rice Research Institute (NRI), Cuttack, has recognized the importance of DSR and has played a key role in developing and popularizing varieties suitable for DSR in India (Table 2). Grain yields under DSR using DSR-adapted rice varieties typically range between 3.0 and 5.5 tons per ha. Although this yield is 20 %-30 % lower than that of lowland varieties cultivated under PTR systems, they are substantially higher about two to three times, than the yields obtained from traditional upland rainfed rice varieties (105).

Future perspectives

DSR offers a resource-efficient alternative to the traditional puddled transplanted rice system. Factors like labour and water scarcity are pushing farmers to shift to direct-seeded cultivation. Enhancing DSR productivity requires a multidisciplinary approach integrating agronomy, breeding, plant protection and social sciences to fully realize its potential.

While current efforts focus on improving individual traits that support direct-seeded cultivation, greater emphasis is needed on developing tailored varieties that pyramid multiple favourable traits. Such an approach would maximize yield potential and enhance the profitability of DSR for farmers. Initiatives like Bayers' DirectAcres Programme, which aims to bring one million ha in India under DSR by 2030, represent a transformative step toward sustainable food security.

Looking ahead, coordinated efforts among research institutions, government agencies and private sector partners will be crucial to accelerate the adoption and broader impact of DSR, ultimately reshaping rice cultivation for greater resilience and sustainability.

Table 2. Varieties suitable for direct-seeded cultivation

Sl. No.	Name	Yield in tonnes/ hectare (t/ha)
1	CR Dhan 200	4.5
2	CR Dhan 201	3.8
3	CR Dhan 202	3.7
4	CR Dhan 203	4.05
5	CR Dhan 204	3.7- 4.5
6	CR Dhan 205	4.1
7	CR Dhan 206	4.8-5.0
8	CR Dhan 207	3.7-4.5
9	CR Dhan 209	3.9
10	CR Dhan 210	3.1
11	CR Dhan 211	4.5-5.5
12	CR Dhan 212	4.4-5.7
13	CR Dhan 214	4.4
14	Sahbhagi Dhan (IRRI 254)	3.8-4.5
15	Sahod Ulan 1 (IRRI 148)	3.7

Conclusion

Direct-seeded rice is emerging as a sustainable alternative to conventional puddled transplanted cultivation, particularly in the scenario of rising water scarcity, increasing labour costs and climate change. The adoption of DSR, while offering remarkable environmental and economic advantages, also exposes plants to challenges in seedling establishment due to waterlogging, heavy weed infestation and lodging, all of which leads to yield instability. Development of next- generation rice varieties tailored for DSR is essential to overcome these challenges. They overcome these challenges through a series of interconnected physiological and morphological adaptations. Traits that are primarily considered include anaerobic germination, early seedling vigour and robust root and shoot architecture for lodging resistance. Advances in molecular breeding like QTL mapping, marker assisted selection and genome editing provide potential tools to enhance the genetic improvement of these traits. Simultaneously, integration of proper crop management practices is essential to utilize the full potential of DSR adapted varieties. With coordinated efforts, DSR has the potential to ensure resource-efficient, profitable and sustainable rice cultivation to ensure the food security of the country.

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Authors' contributions

ASN performed the literature search, collected data and drafted the manuscript. RS conceptualized and designed the review, while SS provided critical feedback and revisions. RS, SM, MU, PK and TE suggested corrections. All the authors read and approved the final manuscript.

Compliance with ethical standards

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