

Quantitative design and realization of green technology for increasing the yield and nitrogen use efficiency of winter wheat

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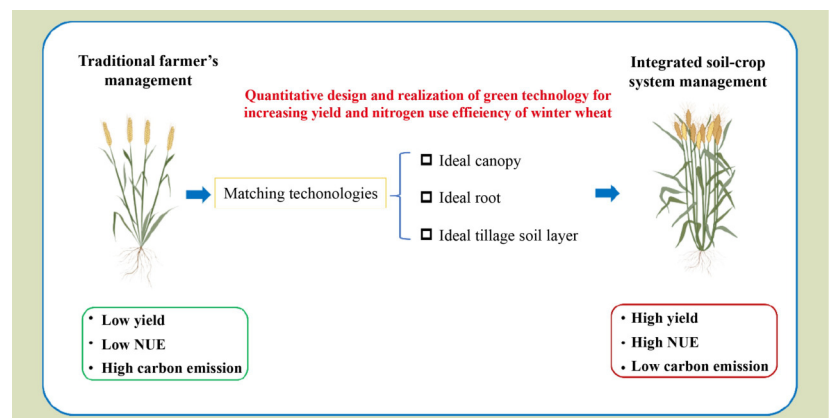
KEYWORDS

Grain yield, green technology, NUE, winter wheat

HIGHLIGHTS

- This study reviewed and advanced a three-stage theory in wheat production in China.
- Key limiting factors affecting yield and NUE in wheat production systems were identified.
- Quantitative design-implementation pathways for wheat green production were developed.
- Integrated management was found to enhance soil quality, grain yield and NUE while reducing carbon footprint.

GRAPHICAL ABSTRACT



ABSTRACT

The development of green technologies for improving winter wheat yield and nitrogen use efficiency (NUE) is crucial for ensuring national food security and reducing carbon footprint. This study outlines China wheat yield progress and establishes a three-stage theory for this. The key constraints from a soil-crop system perspective were identified: population-individual competition, dry matter accumulation and distribution, and soil quality degradation. To address these constraints, an optimized soil-crop system is proposed. (1) Adopting rational dense planting using optimal densities of 330–375 plants m^{-2} for large-spike cultivars and 225–270 plants m^{-2} for medium-spike cultivars to establish robust populations. (2) Enhancing soil quality and reducing carbon footprint by the adoption of straw return combined with a strategy of deep plowing and rotary tillage to improve soil fertility quality, reducing carbon footprint by 1.87 Mg CO_2 eqv ha^{-1} . (3) Using wide-space drill sowing of 6–8 cm sowing belts to minimize interplant competition, coupled with moderate density to stimulate deep-root nitrogen uptake. (4) Optimizing the canopy optimization by delayed sowing (mid-October to early-November) combined with density adjustment enhances light interception efficiency. This integrated soil-crop system management demonstrates long-term effectiveness,

Received November 8, 2024;
Accepted May 5, 2025.

increasing grain yield, NUE and reducing carbon footprint. These findings provide practical solutions for green and efficient production of winter wheat.

1 Introduction

Wheat is one of the most important staple crops globally, providing essential calories and nutrition to billions of people^[1]. In China, where food security is a key national strategy, wheat is crucial for ensuring food supply and stabilizing livelihoods. Over recent decades, through agronomic innovations, policy support and technological advances, China has made great strides in increasing wheat yields^[2–4]. With increasing of population pressure, climate change and limited arable land, there is an urgent need to further increase wheat productivity, especially yield per unit area. However, agricultural production methods characterized by heavy inputs of chemical fertilizers and pesticides and intensive farming have greatly contributed to greenhouse gas emissions, environmental pollution and destruction of land resources^[5,6]. These practices not only undermine the long-term sustainability of agricultural productivity, but also pose a major challenge to China goal of achieving carbon neutrality by 2060^[7].

The challenges for increasing wheat production and efficiency in China are multifaceted, involving not only germplasm resources innovation and the introduction of high-yielding cultivars, but also the optimization and improvement of agronomic measures^[8]. Despite the significant progress that has been made by previous generations to improve yield and resource use efficiency in wheat, multiple factors impede wheat yield improvement^[9,10]. These include the conflict between individual plant development and population uniformity, suboptimal dry matter accumulation and translocation at post-anthesis, and inadequate soil quality to support high wheat yields and high NUE. Addressing these constraints is critical to achieving high yields and efficient resource utilization, especially in the context of China push for carbon-neutral green production.

In this paper we constructed a brief introduction of the wheat yield development in China and limiting factors of wheat yield and NUE increase, and then introduced an ideal characteristic of soil layer, root and canopy structure of wheat, and gave a specific and quantified target for green production. To realize

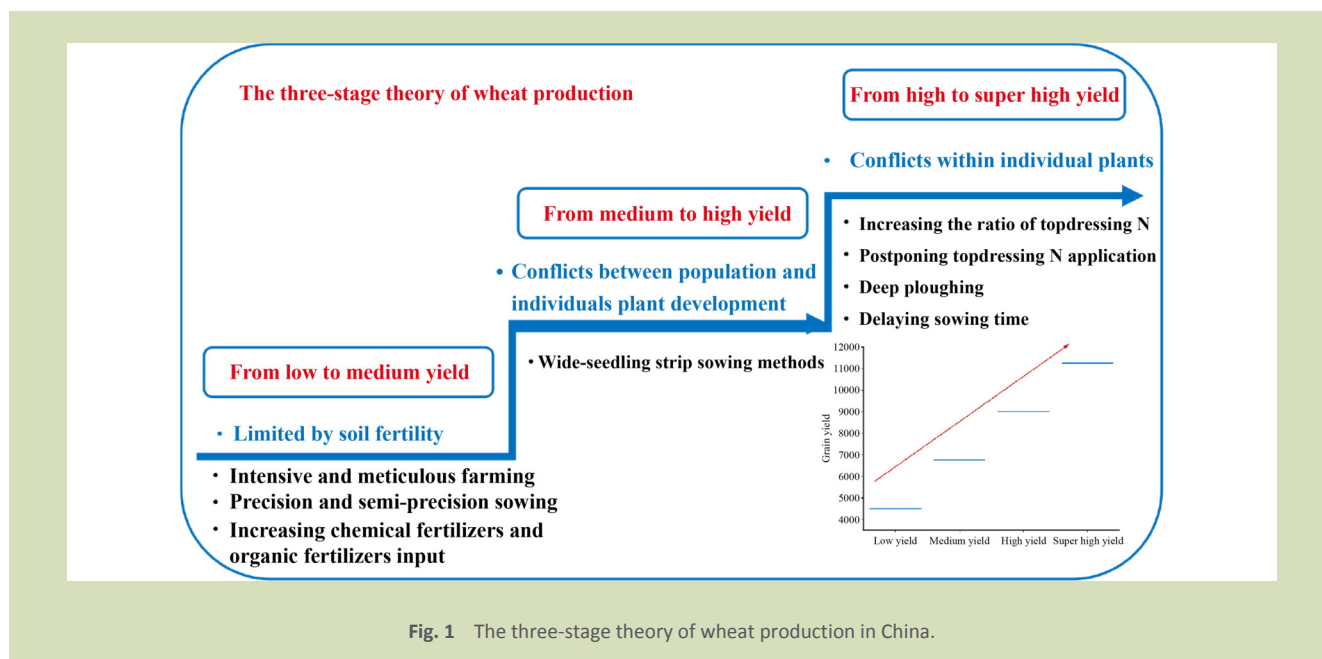
this target, we reviewed the population quantitative basis and the regulation of cultivation management, such as straw return and deep plowing, wide-seedling strip sowing and relatively high plant density, sowing date, to soil structure and carbon storage, root distribution and architecture, dry matter and N assimilation and accumulation, N loss, yield and NUE. An integrated soil-crop system management pattern and its long-term effectiveness on grain yield, N uptake and use, carbon emission and its popularization and application potential were also analyzed.

2 A three-stage theory for development of wheat production in China

The three-stage theory of wheat production in China, proposed by Academician Yu Songlie of Shandong Agricultural University, divided the wheat production capacity improvement in China into three key stages: the transition from low to medium yield, from medium to high yield, and from high to super-high yield (Fig. 1). It emphasizes specific contradictions and key technologies needed to move wheat production from low to medium to high yields, and ultimately to super-high yields, and provides a systematic framework for understanding the progression of wheat yield improvement and the cultivation measures that accompany different yield stage. Each stage has specific agronomic, physiologic and environmental challenges that must be overcome to achieve sustainable yield increases.

2.1 Transition from low to medium yield

At the phase of wheat yield improvement from low to medium yield, the main contradiction existed between the raised requirement of nutrient available from soil along with the wheat yield increasing and the low soil nutrient content. The key interventions included intensive and meticulous farming, increasing chemical fertilizers and organic fertilizers input, precision and semi-precision sowing methods (Fig. 1). These practices aim to create a conducive environment for wheat



growth by improving soil structure, enhancing nutrient and water retention, and optimizing sowing practices. The improved soil environment promotes root development, increases the efficiency of nutrient uptake, and ultimately leads to increased yields. The focus during this stage is to address the fundamental limitations in wheat production, such as nutrient deficiencies and suboptimal planting practices, thus enabling the transition from subsistence-level yields to more stable medium-level yields (Fig. 1).

2.2 Transition from medium to high yield

The improvement of yield from medium to high level emphasizes the balance between population and individual plant development. At this stage, wheat yields are no longer limited solely by soil and basic cultivation practices, but depend on the optimization the relationship between spikes density and individual stem productivity (Fig. 1). The challenge at this stage is to maximize the total number of spikes per unit area while ensuring that individual plants are robust enough to support high spike weight (i.e., relatively high or stable kernel number per spike and kernel weight). Wide-seedling strip sowing methods, which increased the belt of wheat seedlings from 2–3 cm to 8–10 cm by altering the width of the furrow opener moldboard, is crucial in this context for improving spatial uniformity and plant distribution, reducing competition between plants for light, water and nutrients, and optimizing the canopy structure to enhance photosynthetic efficiency^[11,12]. Hence, optimizing canopy structure and

optimal resource allocation among plants becomes a key factor in increasing yield.

2.3 Transition from high to super-high yield

Further increasing wheat yield to super-high level depended mainly on breaching of the internal contradiction within the plant, associated with the source-sink relationship, balance of carbon and nitrogen metabolism, nutrient allocation and remobilization, photosynthesis and senescence characteristics, and the like (Fig. 1). The soil structure of tillage layer, the root and canopy architecture are key components that need to be carefully managed to ensure that the crop achieves maximum yield potential without compromising its physiologic stability or environmental sustainability. Several technologies, such as increasing the ratio of topdressing N and postponing topdressing N application, appropriately postponing sowing date and deep ploughing, has been proved to be effective approaches to mitigate this internal contradiction within wheat plants^[13–15].

Recently, the winter wheat yield level of more than 12 t·ha⁻¹ has been widely reported in Huanghuaihai wheat production region. The highest reported grain yield of winter wheat was also nearly 13.5 t·ha⁻¹ (Fig. 1). The future super-high yield and green production of winter wheat may require a more integrated approach that must coordinate soil health, precise nutrient management, root system and canopy optimization to realize the full production potential of the crop without compromising soil sustainability.

3 Key limited factors for green increase of wheat yield and NUE

3.1 Conflict between individual and population development of plant

A homogeneous population structure is an important cornerstone for achieving high crop yields and efficiency^[16]. A population consists of interconnected and interacting individual plants, with single plants competing for necessary resources such as water, nutrients, heat and sunlight to maximize their vegetative and reproductive growth^[17,18]. The uneven distribution of resources due to uneven field surfaces and human interventions, such as fertilizer application, seeding and irrigation, results in uneven resource availability among individual crops and hinders the formation of a homogeneous population structure^[19,20]. As plant density increases, competition among plants intensifies, negatively impacting root systems, tiller development and nitrogen uptake^[18,21]. At the root level, high-density planting causes physical compression of the rhizosphere space, restricting horizontal root extension and reducing lateral root density^[22]. This results in diminished uptake capacity for deep soil water and nutrients. Regarding tiller development, mutual shading among densely planted vegetation reduces light interception, leading to a decreased red to far-red ratio in the canopy. Plant pigments perceiving this altered ratio signal subsequently regulate stem elongation, leaf area expansion, and tiller reduction through gene expression and physiologic adjustments^[23]. In nitrogen metabolism systems, restricted root absorption under high-density conditions combined with less nitrate reductase activity in leaves impedes glutamine synthesis in vegetative organs^[24]. Consequently, nitrogen translocation efficiency to grains declines, ultimately reducing kernel weight^[25]. Although increasing plant density may enhance total population biomass and yield per unit area, it can adversely affect the production potential of individual wheat plants. Hence, it is necessary to establish a balance between maximizing population yield and maintaining the physiologic health of individual plants.

3.2 Dry matter accumulation and distribution

It is generally believed that the assimilates in the grain are divided into two parts: the dry matter accumulated at pre-anthesis is remobilized to the grain after flowering, and the assimilates synthesized and accumulated at post-anthesis are

translocated to the grain, of which the accumulation of post-anthesis dry matter usually contributes 60%–80% to the grain yield^[26,27]. Therefore, the accumulation and transformation of post-anthesis dry matter make a decisive contribution to grain filling, and insufficient production of post-anthesis dry matter will directly affect grain yield. Insufficient dry matter accumulation at post-anthesis is usually caused by various factors, such as decreased root activity, early leaf failure and insufficient nutrient supply^[28,29]. The health and activity of the root and leaf systems are essential for the N uptake post-anthesis and ensuring sustained production of dry matter during the filling process^[11].

3.3 Insufficient soil quality to support yield improving

Soil quality is the basis for sustainable wheat production. There are significant differences in the physical and chemical properties of soils among different yield-level fields, and these differences have a direct impact on the development of the wheat root system and plant growth^[30–32]. First, low- and medium-yield fields often have higher soil bulk density and tighter soils, which limits root growth and reduces the efficiency of water and nutrient uptake^[33], while the high-yield fields is opposite. Secondly, high-yield fields usually have higher soil porosity, allowing better aeration and drainage, this supports root respiration and microbial activity^[34]. In contrast, low-yield and medium-yield fields tend to have lower porosity, leading to poor aeration and drainage, which can easily cause root hypoxia and inhibit plant growth^[35]. In addition, organic matter content is an important factor in determining soil fertility^[36]. Higher organic matter content in high-yield fields can provide a richer supply of nutrients, improve soil structure and promote microbial decomposition of organic matter, supplying nutrients needed for wheat growth. In contrast, the low organic matter content of low- and medium-yield fields, coupled with the poor water and fertilizer retention capacity of the soil and the decline in microbial activity, further affecting the growth of wheat^[37]. Adequate supply of N in high-yield fields promotes photosynthesis and chlorophyll synthesis in wheat, ensuring healthy plant growth and high yields whereas, with low N content in low- and medium-yield fields, wheat may suffer from yellowing of leaves and reduction of tillers, resulting in significantly lower yields^[38]. Overall, soil physicochemical properties limit the growth and development of the wheat root system, which in turn affects water use efficiency.

4 Quantitative design and technical breakthrough of green production for increasing yield and NUE of winter wheat

4.1 Quantitative design of wheat population or green improvement of yield and NUE

Based on the experience of the three-stage theory of wheat

production in China, further green increase of yield and NUE depends mainly on the systematic optimization of the structure and function of tillage soil layer, root and canopy. According to the development history of wheat production China, targeted yield and NUE level, the requirement of green production, previous research basis and the published data, we designed an ideal system aiming to achieve further green increase of yield and NUE, identified key technologies (Fig. 2) and quantified several key indicators in this system (Table 1). First, tillage soil layer, with characteristic of enhanced capacity of water storage

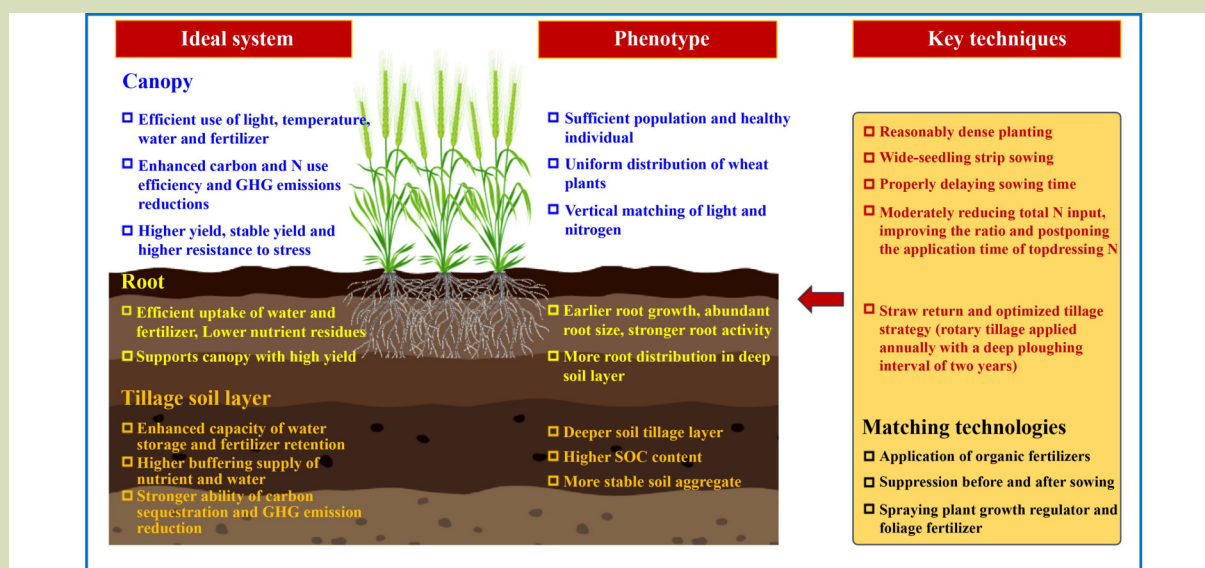


Fig. 2 Ideal design and phenotype characteristic of canopy, root and tillage soil layer for green production with increased grain yield and nitrogen use efficiency of winter wheat and the critical techniques.

Table 1 Quantified key targets of green technology for increasing yield and NUE of winter wheat

Index	Quantified target for wheat green production
Enough population	Big-ear: 330–375 plants m ⁻² (570–630 spikes m ⁻²), Mid-ear: 225–270 plants m ⁻² (675–750 spikes m ⁻²)
Healthy individual	Big-ear: 1.6–1.8 g, Mid-ear: 1.3–1.5 g
LAI	4–5 at early and middle grain filling stage
PAR interception rate	> 90% at early and middle grain filling stage
Post-anthesis DM produced	> 80% grain yield contribution, 40% of total DM produced at maturity
Post-anthesis N uptake	17%–20% grain N accumulation
Root distribution	High-density roots (> 40 cm depth) with high activity
Tillage layer thickness	Deeper than 25–30 cm
SOM	> 20 g·kg ⁻¹ with strong carbon sequestration
Soil aggregate	High large-aggregate ratio with stable structure and increased mean weight/geometric diameters

Note: DM, dry matter; LAI, Leaf area index; PAR, photosynthetic active radiation; SOM, soil organic matter.

and fertilizer retention, higher buffering supply of nutrient and water, stronger ability of carbon sequestration and greenhouse gases emission reduction, is demanded and presents as deeper soil tillage layer, higher soil organic carbon (SOC) content and more stable soil aggregate. Secondly, the root should be capable of efficient uptake of water and fertilizer and lower nutrient residues to support the canopy with high yield and NUE. This required earlier root growth, abundant root size, stronger root activity and greater root distribution in the deep soil layer. Thirdly, in terms of canopy, it requires an ability of efficient use of light, temperature, water and fertilizer, through enhancing utilization of carbon and N, and consequently observe higher and stable grain yield, higher resistance to abiotic and biotic stress, and decreased greenhouse gas emissions. To achieve these targets, based on the previous research results of our research team, several key technologies approach are proposed, including straw return, optimized tillage strategy (rotary tillage applied annually with a deep plowing interval of 2 years), moderately dense planting, wide-seedling strip sowing, properly delaying sowing time, moderately reducing total N input, improving the ratio and postponing the application time of topdressing N (Fig. 2). In addition, some matching technologies including application of organic fertilizers, suppression before and after sowing, spraying plant growth regulator and foliage fertilizer, are also put forward to guarantee the integration and implementation effect of these key technologies. Future research could use life cycle assessment methodology to quantify the carbon footprint associated with these key technologies in wheat production systems, which would establish a scientific foundation for optimizing green, high-yield and resource-efficient cultivation practices.

In addition, we illustrated several quantifiable indicators including the population amount, individual weight, leaf area index, photosynthetically active radiation (PAR) interception rate, root distribution and soil organic matter (SOM) content (Table 1). All of this provides basis and references for the theory and technology innovation of wheat green increase of yield and NUE in the future.

4.2 Realization of green production with synergistically improving grain yield and NUE

4.2.1 The population basis of high yield and high NUE established by reasonably dense planting

Planting density is a cultivation measure that is easier to control in the process of achieving increased wheat yields, and it is also a key factor influencing the structure of wheat

populations and the composition of yields^[39,40]. The most direct effect of increasing planting density is to increase the number of tillers and spikes per unit area^[41]. Several earlier studies have shown that wheat yield increases linearly with increasing planting density and eventually stabilizes at a maximum value^[21,40,42]. Properly increasing plant density of winter wheat could significantly increase total root number and root length density (RLD) at each soil depth, as a result of which enhanced the N absorption from different soil layer, especially from deep soil depth, and consequently increased fertilizer N and soil N accumulation at maturity, N uptake efficiency (UPE; i.e., the ratio of aboveground N uptake to N available from fertilizer and soil) and NUE (i.e., the ratio of yield to N available)^[40]. The improved RLD and strong nutrient uptake capacity endows the dense planting wheat the ability of maintaining high grain yield and increasing NUE decreased N input^[43].

In addition, the improved RLD at deep soil layer under relatively dense planting density is conducive to lower the ratio of soil evaporation to evapotranspiration after jointing, enhance the ratio of soil water consumption below 1 m to total soil water consumption and synchronously increase grain yield and water use efficiency of winter wheat^[44]. Despite the total root numbers per unit area and RLD increased at supraoptimal density while N uptake, NUE and yield stagnated^[41], reasonable dense planting is undeniably one of the simplest strategies to improve wheat yield^[45,46] and also is beneficial to establish enough population basis for further improving grain yield and NUE of winter wheat.

4.2.2 Straw return and a strategy of deep plowing plus rotary tillage improved soil fertility and carbon sequestration capacity

At present, straw return to field has become a more mature and widely used technology (Fig. 3). It has a high potential of land productivity improvement and fertilizer substitution for wheat production in China^[47]. Application of straw return significantly decreased the soil bulk density and increase the soil total porosity, not only in topsoil (0–40 cm) layers but also in subsoil (40–120 cm) layers, and consequently promoted the exploration of root system and the proportion of root system in subsoil layers^[48]. Straw return also alters the soil microbial habitat and provides a rich source of carbon for microbial activity, thereby increasing the variety and abundance of soil microbes, which is critical for organic matter decomposition and nutrient cycling^[49–52], therefore enhance soil quality by increasing SOC content and improve nutrient availability of soil^[53–55]. The return of wheat and maize straw in winter

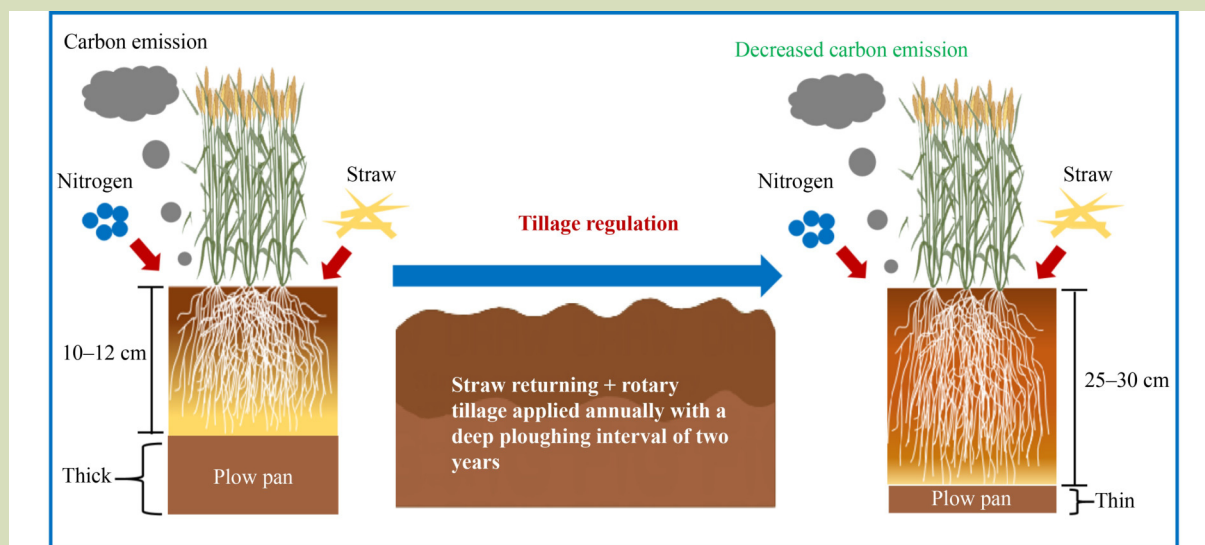


Fig. 3 The key techniques of green, yield-enhancing and efficiency-enhancing of wheat for straw return to fields and a strategy of deep plowing plus rotary tillage, which is a combination of two consecutive years of rotary tillage with a third year of deep tillage.

wheat-summer maize cropping system significantly increased the contents of SOC, mineral nitrogen and available phosphorus, as well as soil urease, alkaline phosphatase activities and microbial diversity^[56]. In the wheat-maize rotation area, the total amount of maize straw returned to the field could theoretically substitute the chemical fertilizers input at rate of $39.4 \text{ kg}\cdot\text{ha}^{-1} \text{ N}$, $28.9 \text{ kg}\cdot\text{ha}^{-1} \text{ P}_2\text{O}_5$ and $110 \text{ kg}\cdot\text{ha}^{-1} \text{ K}_2\text{O}$ in the wheat production season, and in the rice-wheat rotation area, the total amount of rice straw returned to the field could theoretically substitute chemical fertilizers input at rate of $29.9 \text{ kg}\cdot\text{ha}^{-1} \text{ N}$, $17.8 \text{ kg}\cdot\text{ha}^{-1} \text{ P}_2\text{O}_5$ and $145 \text{ kg}\cdot\text{ha}^{-1} \text{ K}_2\text{O}$ in the wheat production season^[57]. With straw return, the required N input ($233 \text{ kg}\cdot\text{ha}^{-1}$), under which the soil N pool could reach balance, was significantly lower than that without straw incorporation ($308 \text{ kg}\cdot\text{ha}^{-1}$)^[58]. These positive effects of straw return were beneficial to increased aboveground N absorption, grain yield, UPE and NUE of winter wheat^[38].

Appropriate tillage practices are crucial for enhancing soil health, increasing grain yield and NUE in winter wheat cultivation^[56]. Long periods of continuous use of rotary tillage would create a hard plow pan in the 10–25 cm soil layer (Fig. 3), which may stop roots from reaching deeper soil layers^[47]. Deep plowing can break this plow pan (Fig. 3), promote the expansion of the root system to a deeper layer, increase the absorption area of the root system, facilitate access to deep N and water, and enhance the water use efficiency and NUE in wheat plants^[59]. Deep tillage also could increase SOC

content in the 10–40 cm soil layer^[13,56]. However, continuous deep plowing is relatively expensive and can destroy soil structure and lead to organic carbon loss^[60,61], which negatively impacts sustainable agriculture^[62].

Base on the positive effect of straw return and deep plowing on soil quality and wheat plant growth and the actual production conditions, an optimized tillage strategy (straw return plus rotary tillage applied annually with a deep plowing interval of 2 years), was locally implemented from 2012 (Fig. 3). Under straw return condition, this optimized tillage strategy observably increased organic matter content in 10–30 cm soil layer, decreased bulk density in 0–20 cm soil layer, and increased the total porosity in 0–20 cm soil layer and capillary porosity in 10–30 cm soil layer^[63]. Compared with the common tillage practiced by farmers (rotary tillage annually and $300 \text{ kg}\cdot\text{ha}^{-1} \text{ N}$ input), the optimized tillage strategy with $225 \text{ kg}\cdot\text{ha}^{-1} \text{ N}$ input observed higher SOC stock and balance distribution in 0–30 cm soil layers and decreased the carbon footprints (Fig. 3) by $1.87 \text{ Mg}\cdot\text{ha}^{-1} \text{ CO}_2 \text{ eqv}$ ^[56].

4.2.3 Wide-space drill sowing modified root architecture of dense planted winter wheat

Standard drill sowing is a common planting technique for wheat with simple operation^[64]. However, it is difficult to further increase the spikes density by increasing the sowing rate due to the fierce competition among individual plant because of narrow strip seedling belt (generally 2–3 cm) and small plant spacing^[65]. However, wide-seedling strip sowing

(seedling strip width of 6–8 cm) weakened this competition^[66], and the optimal plant density for improved grain yield and NUE of winter wheat was significantly higher than drill sowing^[65]. In addition, wide-space drill sowing (WSD sowing) combining properly dense planting modified wheat root architecture, enhanced N uptake from deep soil layer and accumulation higher N at maturity compared with drill sowing^[67]. In this case, the increased intra-row spacing of the WSD sowing resulted in increases in the number of tillers and roots, aboveground dry matter per unit area and root to shoot ratio, as a result of which the total root weight, RLD and root surface area density increased at each soil layer. Stable isotope (¹⁵N) labeling showed that the N absorption from different soil layer was increased under WSD sowing, but it increased N uptake from the 0–40 cm soil layer mainly through increasing root amount, while the increased N uptake from 40 to 80 cm and 80 to 120 cm soil layers was primarily due to the synchronous improvement in root size and fertilizer uptake efficiency^[67].

Meanwhile, under dense planting conditions, the root system is forced to expand into deeper soil to access more nitrogen resources due to the increased number of plants per unit area and the increased competition for nitrogen among individuals^[68]. It also has been verified that properly dense planting also enhanced N uptake from medium and deep soil layer owing to the increased RLD at corresponding soil layer^[41]. All of these enlightens the importance of root in subsoil layer and the future regulating targets of root architecture for more efficient nutrition uptake, further higher grain yield and NUE.

4.2.4 Optimal canopy architecture construction for further higher grain yield and efficient use of N and photosynthetically active radiation

In general, although increasing plant density of winter wheat would increase spikes number per unit area, however, the grain number per spike and individual grain weight often have a decreasing trend^[21,40]. This downward trend is hard to change according to previous theoretical research and practical experience, and the extent of this reduction and its tradeoff with the increment of population amount always decides the change in yield of winter wheat. Slowing down this decrease may be an efficient approach to seek higher grain yield. Compared with the drill sowing combining with low or medium plant density, WSD sowing significantly improved green leaf area index, PAR interception, canopy apparent photosynthesis (CAP), delayed leaf senescence, extended the duration of high-value CAP period, and radiation use

efficiency, and ultimately lead to observably increase in post-anthesis dry matter production^[11,12,66,69]. Therefore, the relatively sufficient supply of photosynthate alleviated the negative effect of increasing spikes per unit area on decreasing single spike weight and greater grain yield increase was achieved^[65]. Another sowing method aiming to promote uniform plant distribution, tridimensional uniform sowing, with relatively dense sowing also slows down the reduction of grain number per spike and individual grain weight and markedly improved grain yield of winter wheat compared with the drill sowing^[70]. This also confirm that the future further yield improvement of winter wheat may be more dependent on the uniform distribution of plants.

For NUE, although reasonably increasing plant density would significantly improve NUE of winter wheat through enhancing N accumulation and UPE, the UTE (i.e., the ratio of grain yield to aboveground N uptake at maturity) often has a decreasing trend owing to the lower N harvest index^[40]. This downward trend is also difficult to change and its extent and tradeoff with the increased UPE would also decides the change in NUE of winter wheat. Slowing down this decrease and efficient use of absorbed N heavily depends on the canopy photosynthesis characteristic, because leaf and canopy photosynthesis per unit N is extremely critical to improve UTE^[71]. Compared with the drill sowing combining with low or medium plant density, the raised PAR interception and RUE may be the main reason that WSD sowing alleviated the negative effect of increasing UPE on decreasing UTE, and consequently improved NUE.

WSD sowing may be used to decrease N inputs without penalizing yield due to its superior nutrient absorption capacity^[67]. According to the difference response of yield, N₂O emission and N loss to N fertilizer amount between WSD sowing and drill sowing from^[11,72]. We simulated the demanded N fertilizer at grain yield levels of 7.5–11.5 t·ha⁻¹ under WSD and drill sowing, respectively. The results showed that when the same yield level was obtained, the required N fertilizer was 22.3–74.5 kg·ha⁻¹ lower under WSD compared to drill sowing. NUE was correspondingly improved by 3.82–6.65 kg·kg⁻¹. Meanwhile the N₂O emission and N loss was reduced by 0.05–0.33 kg·ha⁻¹ N and 7.29–27.9 kg·ha⁻¹ N, respectively. This confirmed the green production potential of WSD sowing in further improvement of yield and NUE.

Postponing sowing in WSD sowing wheat to a certain degree had no significant influence on grain yield^[73], but delayed sowing presented high potential in increasing UTE and lodging resistance. First, delayed sowing increased grain number per spike resulting from higher floret survival rate due to

enhancing partitioning of assimilates to the spikes through modifying hormone homeostasis between developing spikes and stems^[74] and the improvement of grain number per spike originated principally from an increased grain number in the apical sections of spikes and in distal positions on the same spikelet^[75]. The improvement of grain number per spike offset the reduction of spike per unit area because of the decreased accumulated temperature and therefore stable grain yield was obtained under delayed sowing^[76]. Secondly, although delayed sowing decreased total N uptake at maturity, but also decreased the N redundancy, and meanwhile on a timescale enhanced N absorption from jointing to anthesis, therefore the wheat plant was in near-optimum N conditions (N nutrition index of about 1) after N fertilizer topdressing at jointing and UTE was markedly improved^[77]. In addition, delayed sowing optimized N allocation at crop-canopy level, whole-plant level, leaf layer level and cellular level, through increasing N content in individual plant, and boosting N allocation to upper leaves (flag and second leaves), enhancing leaf mass per area and specific green leaf area N in upper leaves, and improving N proportions allocated to ribulose-1,5-bisphosphate carboxylase/oxygenase in upper leaves, and consequently improved canopy photosynthetic N-use efficiency and UTE^[14]. Thirdly, in terms of ensuring stable wheat yield, lodging resistance was observably improved under delayed sowing through a decrease in the culm height at the center of gravity and enhancement in filling degree and tensile failure strength of the base internode^[73]. This was mainly because that the earlier and higher expression of levels of key genes (*TaPAL*, *TaCCR*, *TaCOMT*, *TaCAD*, and *TaCesA1*, -3, -4, -7 and -8) and enzyme activities (*TaPAL* and *TaCAD*) related to lignin and cellulose biosynthesis under delayed sowing resulted in higher accumulation rates, higher maximum accumulation contents, and longer accumulation duration of lignin and cellulose during the stem elongation stage^[78].

5 Integrated soil-crop system management approach and its long-term influence on soil quality, grain yield and NUE

Integrated soil-crop system management (ISSM) is an efficient approach to substantially increase crop yield and simultaneously increasing NUE and reducing environmental footprints^[79]. An ISSM approach was implemented, incorporating rational dense planting, WSD sowing, appropriately delaying sowing time, optimized N input, straw return and deep plowing. To evaluate the effectiveness of ISSM,

a long-term field experiment was conducted from 2008 in Tai'an City, Shandong Province. The long-term application results showed that the ISSM approach significantly decreased soil bulk density of surface 0–20 cm soil, improved the alkali-hydrolyzable N, and available potassium of surface soil^[80], maintained soil aggregate stability, increased content of SOM through increasing organic carbon and total nitrogen of the light fraction and the particulate organic matter fraction (POM), improved SOM quality by increasing the proportions of light fraction and POM and the ratio of organic carbon to total nitrogen in SOM, and consequently increased soil integrated fertility index by 25.6% and 28.9% in the 0–20 and 20–40 cm soil layers, respectively^[81]. In addition, ISSM approach could enhance carbon-related functional groups, such as aromatic hydrocarbon degradation and hydrocarbon degradation, to increase the SOC content, and improved the structure and the co-occurrence network density of soil microorganisms at the vigorous period of crop growth^[82]. All of these positive regulations are beneficial to wheat growth, yield formation, efficient N use and reducing N loss^[83,84].

Compared with the common management practices of farmers, the whole plant at anthesis stage and spikes at maturity stage under ISSM mode were in balance of nitrogen supply and demand^[80,84]. Therefore, the ISSM approach enhanced radiation capture^[85] and N uptake and use^[83], and obviously increased grain yield, UPE, UTE, NUE, and N recovery efficiency by 22.5%, 43.9%, 3.6%, 49.2%, 48.2%^[80]. In addition, the ISSM approach significantly decreased inorganic N accumulation in the 0–100 cm soil layer, decreased the N surplus amount and N surplus rate by 44.1% and 26.7%^[80], respectively, and also decreased the abundance of bacteria associated with GHGs emissions^[82].

However, by increasing plant density or wide-seedling strip sowing improved NUE both through increasing UPE, UTE was always decreased or only maintained^[40,86]. Despite delayed sowing or the ISSM approach improved UTE, but both led to decreased N accumulation^[14,83]. Therefore, improving UTE may be an effective measure to further enhance NUE. In general, UTE characterizes the process of N assimilation and the efficiency of N to C fixation in plants from a physiologic perspective^[72]. N absorbed during the vegetative growth stage of wheat is used for canopy establishment, including the structural and functional composition of the canopy, especially the photosynthetic apparatus^[87]. As wheat grain yield primarily comes from photosynthetic products generated in flag leaf during the grain filling stage, it suggests that UTE at whole-plant level is contingent upon leaf nitrogen allocation and leaf photosynthesis during this stage^[14,88]. Hence, the

future research focus could center on enhancing the allocation of N in leaves to optimize use efficiency and grain productivity across the entire plant. However, this approach has significant challenges because the phenotypic plasticity responses to high densities correlated strongly with those to low-light^[21], the shade-avoidance syndrome of wheat plant may demand more N allocation for radiation capture. This approach also proves the importance of overcoming the internal constraints within the plant itself when we attempt to improve grain yield from a high- to a super-high level.

6 Conclusions

Reasonable dense planting established population basis of high yield and high NUE of winter wheat. Optimizing tillage strategy (straw return plus rotary tillage applied annually with a deep plowing interval of 2 years) could improve the soil characteristic in 0–40 cm layer and support the relatively dense population. WSD sowing not only modified root architecture and increased N uptake, enhanced the interception and

utilization of PAR, and improved CAP and yield, but also presented large potential in reducing carbon footprint and N loss. Delayed sowing improved stability of yield and NUE under WSD sowing through increase grain number per spike, UTE and lodging resistance. Theoretical analysis and production practice have shown that the ISSM approach has considerable potential in green production with synergistic improvement in grain yield and NUE. Sustained attention should be given to its larger scale application in the future. The regulation of UTE at canopy and individual level requires special attention in future for further increase of yield and NUE. The current validation of ISSM is limited to the Huanghuaihai wheat production region. The applicability of technology to other agro ecological zones with distinct climatic and edaphic conditions requires further investigation. Additionally, the carbon footprint throughout the wheat life cycle and economic costs associated with ISSM implementation remain to be evaluated. Future research should prioritize quantifying both the emission reduction potential and economic benefits of this management system.

Acknowledgements

This study was supported by National Key Research and Development Program of China (2023YFD2300200), National Major Agricultural Science and Technology Project, China (NK202218080315), Key Research and Development Program of Shandong Province, China (2023TZXD086, LJNY202103, 2022LZGC005-402), College Youth Innovation Technology Support Program of Shandong Province, China (2022KJ242).

Compliance with ethics guidelines

Chuan Zhong, Wei Zhou, Wuyang Yu, Mingrong He, Zhenlin Wang, Yuanjie Dong, and Xinglong Dai declare that they have no conflict of interest or financial conflicts to disclose. All applicable institutional and national guidelines for the care and use of animals were followed.

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