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Review

The next Green Revolution: integrating crop architectype and physiotype

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In the middle of the last century, the Green Revolution dramatically increased crop yields and transformed global agriculture. As current food production is increasingly challenged by the demands of the growing population, climate change, and environmental degradation, a new Green Revolution is urgently needed. This Review highlights recent progress in defining the morphological ideotypes of four major crops, and proposes essential physiological traits critical for crop improvement and environmental adaptation. We introduce two concepts: the 'architectype' representing optimized morphological features, and the 'physiotype' encompassing improved physiological traits. By integrating these concepts through advanced genomic technologies and precision management practices, the next Green Revolution could potentially enhance crop yields and resource use efficiency by over 20–30%, thereby ensuring sustainable food production.

Highlights

The Green Revolution must evolve to meet global food demand in times of climate change and global crisis.

The architectype represents an important breeding target to secure yields under varying climatic and environmental conditions.

Optimized physiological traits, defined as the physiotype, need to be integrated with optimized morphological traits to enhance yield potential, reduce resource input, and maximize environmental resilience.

The synergy between ideal architectype and optimal physiotype can enable a new Green Revolution driven by advancements in genomics, transgene, genomic selection, genome editing, molecular design, and precision management practices.

Emerging technologies, including high-throughput phenotyping, multi-omics approaches, machine learning, and artificial intelligence, will facilitate the discovery of gene sets for critical traits and accelerate the breeding of next-generation crop varieties.

Challenges in enhancing crop production

The growing world population and rising demands for meat and dairy products necessitate continuous improvements in crop production for food and feed. Despite significant yield gains during the first Green Revolution in the 20th century (Box 1), recent decades have seen stagnation or even declines in yield for major crops in many regions (Figure 1). A number of factors such as climate change, soil degradation, water scarcity, suboptimal management practices, and socioeconomic constraints contribute to this plateau, and raise serious concerns about food security in the future [5]. In view of accelerating global warming and environmental degradation, improving crop yields and, at the same time, enhancing the resilience of crop plants to abiotic stresses (e.g., drought, heat, and flooding) and reducing the adverse environmental impact of agriculture, represents one of the biggest challenges that mankind faces in this century. This challenge is particularly pressing in sub-Saharan Africa and densely populated countries such as China and India. Advances in genetic and genomic technologies, and new interdisciplinary approaches present opportunities for a new Green Revolution to meet future food demands with a reduced environmental footprint.

This Review examines recent progress with improving morphological features of the **ideotypes** (see Glossary) for four key crops: rice, wheat, maize, and soybean. It summarizes the physiological traits involved in determining crop yields under changing climatic conditions, and explores strategies for developing elite ideotypes using advanced genetic and genomic methods, computational tools, and precision agronomy to achieve sustainable food security.

The ideotype of a crop

The term 'ideotype', introduced by C. M. Donald in 1968 during the first Green Revolution, refers to an idealized plant model designed to maximize biomass or product yield of crops (e.g., grain, oil, or other useful outputs) when cultivated under specific conditions [6]. The concept

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Box 1. The first Green Revolution

The first Green Revolution, initiated in the 1960s, profoundly enhanced global crop yields and saved over a billion people from starvation within 50 years. It was primarily driven by the breeding of semi-dwarf varieties of wheat and rice. Average yields per hectare in developing countries increased by 208% for wheat, 109% for rice, and 157% for maize between 1960 to 2000, with Southeast Asia, India, and China experiencing particularly remarkable yield surges [1].

Beyond high-yielding varieties generated by hybridization and genetic technologies (e.g., transgenic methods and marker-assisted breeding), crop yield increases were supported by advancements in agronomic management, including irrigation systems, and essential agrochemicals (fertilizers, herbicides, and pesticides). Crucial genes underpinning GRV function in GA-related pathways, such as *Reduced height 1* (*Rht1* or *Rht-B1b*) and *Reduced height 2* (*Rht2* or *Rht-D1b*) in wheat [2] and *semi-dwarf 1* (*sd1*) in rice [3]. These genes confer a semi-dwarf phenotype with increased tiller numbers, thus enhancing resistance to lodging, increasing the harvest index, and improving mechanical harvesting efficiency.

However, the reduced NUE of GRVs caused by their GA deficiency requires high fertilizer input, which contributes to environmental degradation and poses a significant challenge to the sustainability of agriculture [4]. In the face of increasing food demands and rising concerns about climate change and environmental degradation, holistic approaches towards optimizing the ideotype of crop varieties offer a promising strategy to ensure long-term food security while minimizing the environmental impact of agriculture.

emphasized the strategic selection of traits that enhance crop productivity and efficiency, thus going beyond the natural adaptations shaped by evolution. Ideotypes integrate morphological, physiological, and biochemical characteristics that collectively exceed the performance of existing cultivars.

A central component of ideotype design is plant architecture, which, among other features, determines the efficiency of crops to capture resources such as light, water, fertilizer at both the level of the individual and the level of the population (canopy). As our understanding of crop physiology and the available breeding technologies continue to advance, the concept of the ideotype evolves, by incorporating additional traits such as nutrient use efficiency, stress resilience, and pest resistance. In the future, new challenges driven, for example, by climate change, resource limitation, and increasing food demands will need to be considered as well. Consequently, the development of crop ideotypes is an ongoing and dynamic process, in which the growing needs for higher productivity and more sustainable agricultural practices need to be considered properly.

Ideal architectypes for major crops

The ideal ideotype differs between crop species. For example, tillering is a critical trait in most cereals (except maize), whereas branching is crucial in many dicots. Nonetheless, the ideotypes for all major crops share some common traits, including short stature with strong lodging

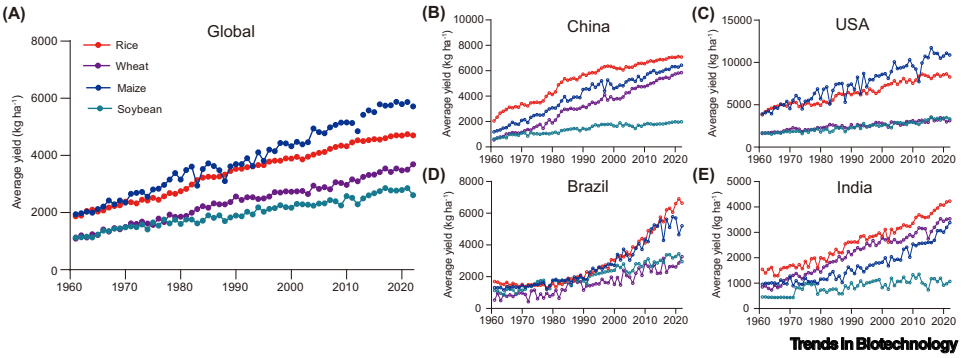

Figure 1. Average yield of four major crops from 1960 to 2022. (A) global; (B) China; (C) USA; (D) Brazil; (E) India. Yield data were obtained from FAOSTAT (https://www.fao.org/faostat/en/#data/QCL).

Glossary

Anthesis-silking interval (ASI): the time period between pollen shed (anthesis) and silk emergence in maize, serving as a key indicator of reproductive synchrony affecting grain yield.
Architectype: key morphological traits forming an ideal plant structure for yield optimization.
Awn: a bristle-like extension arising from the lemma, aiding seed dispersal and potentially enhancing photosynthesis and drought tolerance.
Crop Pan-genome Decoding Project: a large-scale initiative integrating multi-omics and germplasm resources to map the genetic diversity of major crops, facilitating comprehensive gene discovery and enabling precision breeding.
Crop Phenome Project: a systematic initiative to characterize crop phenotypic traits (morphological, physiological, and biochemical) and their dynamic responses to environmental factors throughout the entire growth cycle, accelerating precision breeding for enhanced stress resilience and yield.
Culm: the main stem of cereals (e.g., wheat), consisting of nodes and internodes, responsible for structural support and the transport of water, nutrients, and assimilates.
Ideotype: an idealized plant model with optimized traits for maximum dry matter production and yield under defined environmental conditions.
Nitrogen-use efficiency (NUE): the efficiency of nitrogen absorption and utilization for plant growth and yield.
Panicle: the reproductive organ of rice and some other grasses, consisting of the rachis, primary and secondary branches, and spikelets, responsible for bearing grains.
Physiotype: the physiological characteristics of plants under specific environmental conditions.
Tassel: the male reproductive organ at the top of the maize plant, composed of a main axis, branches, spikelets, and florets, responsible for producing pollen.
Tiller: a lateral shoot emerging from an axillary bud at the basal nodes of cereals and other grasses, classified as productive (bearing grain) or unproductive.
Water-use efficiency (WUE): the ratio of biomass or yield to water consumed, reflecting a plant's ability to use water efficiently.

resistance, compact and erect leaves allowing more **tillers** or branches to develop, medium-sized reproductive organs (that contribute to lodging resistance while supporting efficient reproduction), high yield, high cropping density tolerance, efficient photosynthesis, high nutrient use efficiency, and (abiotic and biotic) stress resilience.

The species-specific aspects of the ideotype address the unique biological properties and agronomic needs of the crop. The term 'ideal **architectype**' refers to the architectural component of the ideotype, and traditionally comprises key morphological traits that directly determine yield formation. Later, we summarize the desired characteristics of the architectypes of four major crops – rice, wheat, maize, and soybean – by synthesizing previous studies and identifying traits requiring further optimization to facilitate ideotype design and benefit agricultural production. Previously identified genes related to traits that are part of the ideal architectype of these crops are listed in Table 1.

Rice

The introduction of semi-dwarf varieties during the first Green Revolution in the 1960s and the subsequent breeding of hybrid rice in the 1970s represented milestones in worldwide rice cultivation. These advances were largely driven by the utilization of mutant alleles of the *sd1* gene and the development of a cytoplasmic male sterility (CMS) system. Professor Yuan Longping's pioneering work on hybrid rice has contributed substantially to global food security by facilitating the rapid commercialization of the new varieties. However, rice yield growth has plateaued in recent years, highlighting the need for a new leap forward. The Green Super Rice project, launched by the International Rice Research Institute (IRRI), the Chinese Academy of Agricultural Sciences, and the Bill & Melinda Gates Foundation, aims to achieve high and stable yields with reduced inputs and enhanced stress resistance. In China, the 'super hybrid rice' strategy integrates ideotype optimization with heterosis utilization, featuring tall erect-leaf canopies, lower **panicle** positions, and larger panicles to maximize yield potential [7].

Desired traits that, together, would contribute to higher yields include (i) moderate plant height (90–110 cm) with sturdy stems for lodging resistance and efficient photosynthate translocation; (ii) erect, thick, dark green flag leaves for enhanced photosynthesis; and (iii) the 'stay-green' trait characterized by delayed leaf senescence to extend the duration of photosynthetic carbon assimilation [8,9]. The balance between tiller number and spikelet number per panicle represents another critical determinant of rice yield. An optimal configuration would involve 8–10 productive tillers (in the absence of any unproductive ones), to minimize resource competition [10]; however, the ideal tiller number can vary significantly across different latitudes, as the heading date directly influences tiller formation. Compact tiller angles to enhance light interception and photosynthetic efficiency are favored for maximizing yield per unit growing area [11]. Improved grain yields can be achieved through increased panicle branching and grain numbers, as facilitated, for example, by tissue-specific manipulation of brassinosteroid (BR) contents and/or signaling [12]. Grain-filling rates can be accelerated by ensuring efficient assimilate flow from leaves to grains, which would support the formation of large, plump grains and lead to harvest indexes above 0.65 [13]. Additionally, a deep and robust root system – characterized by thick, branched roots and a high root-to-shoot ratio – would support strong anchoring of plants in the soil, efficient water uptake and nutrient acquisition, and enhanced stress resilience [14]. Collectively, these features should lead to substantially increased productivity and improved sustainability of rice production (Figure 2A).

Wheat

A wheat ideotype was first proposed by Donald [6], and encompassed (i) short, strong stems, (ii) few, small and erect leaves, (iii) large, erect ears with **awns**, and (iv) a single **culm**. To further enhance yield and lodging resistance, an ideal plant height of 70–80 cm with optimized internode

Table 1. Examples of known genes involved in the control of the ideotype of rice, maize, wheat, and soybean

Crop	Trait	Gene name	Function	Refs
Rice	Tiller	*OsDHT1*	*dht1* mutants show dwarfism and increased tiller numbers	[81]
		OsNAL11	*NAL11*$^{-923del-1552\ allele}$ exhibits relatively few tillers, thick stems, and large panicles	[82]
		OsRCN22	*rcn22* mutants display reduced tiller number	[83]
	Panicle/grain	*OsIPA1/SPL14*	A point mutation in *OsSPL14* results in enhanced lodging resistance, increased grain number per panicle and grain yield	[84]
		OsSPL13	Overexpression of *OsSPL13* increases grain size, panicle length and branching, and grain number per panicle	[85]
		OsmiR396ef	*mir396ef* mutants show enhanced panicle number and grain size, lead to improved yield	[86]
		OsLARGE2	*large2* mutants exhibit larger grains and increased grain number, with thick culms	[87]
		OsDREB1C	Overexpression of *OsDREB1C* increases grain weight and grain number per panicle	[13]
		OsGN1.1	NIL-*GN1.1*^{B} increases grain number per panicle and yield	[88]
		OsBRD3	Activated expression of the *BRD3* gene increases the number of secondary branches, grain number, and yield	[12]
		OsGNA	Overexpression of *OsGNA* increases panicle branch number, grain number per panicle, and yield	[89]
	Plant height	*SD1*	Mutations in *SD1* reduce rice height and enhance lodging resistance	[3]
		SBI^{SV14} allele	Overexpression of *SBI*^{SV14} decreases plant height and improved lodging resistance	[90]
		OsMYB110	Inactivation of *MYB110* increases culm diameter and bending resistance, leading to enhanced lodging resistance despite increased plant height	[91]
		OsKAN1	*OsKAN1* mutants present semi-dwarf and rolling leaf phenotypes	[92]
	Leaf	*OsPROG1*	Loss of *PROG1* gene function results in erect leaves, increased grain number per panicle and higher yield	[93]
		OsURL1	*url1* mutants display an upright growth phenotype that makes them suitable for planting under high-density conditions	[94]
		OsFLP	*OsFLP* mutation leads to increased leaf angle	[95]
Wheat	Tiller/spike number	*TaPIL1*	Overexpression of *TaPIL1* reduces wheat tiller number and increases plant height	[96]
		TaCol-B5	Overexpression of *TaCol-B5* increases tiller number, spikelet number, spike length, and yield	[20]
		DUO-B1	*DUO*-B1 knockout mutants exhibit increased spikelet number	[97]
	Grain number per spike	*TaMYB72*	*TaMYB72* mutation increases spike length, grain number per spike, the thousand grain weight, and yield	[98]
		TaFT-D2	*TaFT-D2* mutation increases spike number, spikelet number, and yield	[99]
	Plant height	*Rht1*, *Rht2*	*Rht-B1b* (*Rht1*) and *Rht-D1b* (*Rht2*) alleles confer a semi-dwarf phenotype with reduced plant height and enhanced lodging resistance	[2]
		ZnF	*ZnF* deficient mutants display reduced plant height	[80]
		Rht8	*Rht8* mutation decreases plant height	[100]
	Leaf	*TaSPL8*	The *TaSPL8* knockout mutant exhibits erect leaves and increased spike number	[101]
	Root	*TaSNAC8-6A*	Overexpression of *TaSNAC8-6A* promotes lateral root development	[102]
Maize	Plant height/ear height	*ZmPIF3.3*	Mutations of *ZmPIF3.3* leads to a significant reduction in ear height and plant height	[103]
		ZmTE1	Knockout of *ZmTE1* significantly shortens internode length and leads to lower plant height	[104]
		ZmACS7	Mutations in *ZmACS7* result in a reduced plant height and larger leaf angle	[105]
		ZmBELL10	*ZmBELL10* regulates the number of internodes, internode spacing, and lodging resistance	[106]
		ZmCRY1b	Overexpression of *ZmCRY1b* significantly reduces plant height and ear height	[107]
		ZmCPK39	*ZmCPK39* mutation decreases plant height	[108,109]
		ZmPUP4	Knockout of *ZmPUP4* represses internode elongation and decreased plant height	[110]
	Leaf	*Lac1*	*Lac1* knockout plants show 'smart-canopy' properties with upright leaves in the upper canopy, and relatively unfolded middle and lower leaves	[23]

Table 1. (continued)

Crop	Trait	Gene name	Function	Refs
		ZmIDD14, ZmIDD15	*ZmIDD14* and *ZmIDD15* double mutations lead to a smaller leaf angle, reduced plant height, and ear height	[111]
		bHLH30	Upon *bHLH30* mutation, the upper leaf angle becomes smaller	[112]
		TU1	Knockout of *TU1* increases the number of leaves above the ear, leading to increased yield	[113]
	Ear	*KRN2*	Knockout of *KRN2* increased kernel numbers per ear and grain yield	[114]
		EAD1	Overexpression of *EAD1* led to greater ear length and kernel number per row	[115]
		YIGE1	Overexpression of *YIGE1* increased ear length and kernel number per row, thus enhanced grain yield	[116]
		ZmACO2	*ZmACO2* loss-of-function lines showed an increase in ear length, kernel number per row, and ear weight	[117]
	Root	*ZmPILS6*	*ZmPILS6* mutations cause reduced root network area and suppressed lateral root formation	[29]
		ZmYUC2/4	The *Zmyuc4* single mutant and the *Zmyuc2/4* double mutant exhibit defects in the gravitropic response, thus leading to an enlarged brace root angle	[118]
Soybean	Internode	*DT1*	A recessive *dt1* allele hastens the termination of apical stem growth, thus decreasing both plant height and the number of nodes	[119]
		DT2	$Dt2^{CR}$ lines exhibit increased branch number, plant height, and stem node number	[30]
		RIN1	*rin1* mutants show less node number, shorter internode length, and reduced plant height	[31]
		GmEID1	*Gmeid1* mutants presents shorter internodes, increased node number and branching, with greater yield	[120]
		TOE4b	Overexpression of *TOE4b* decreases plant height, increases the number of nodes and branches, and increases pod number and yield	[121]
	Petiole	*GmILPA1*	Knockout of *GmILPA1* led to larger leaf petiole angle and shorter petiole	[122]
	Pod and seed	*GmPP2C-1*	The *PP2C-1* elite allele enhances seed size and weight	[123]
		GmMFT	*GmMFT* overexpressing plants show a slight increase in seed length and a significant increase in the 100-seed weight	[124]
		miR396	*miR396* mutants have significantly larger seeds, more pods, and higher yield	[125]

proportions has been proposed, slightly smaller than the 90 cm standard of the first Green Revolution [15,16]. Short basal internodes with larger diameters, combined with gradually increasing lengths and decreasing diameters toward the apex, would improve plant stability and biomass translocation efficiency [17]. Strengthening stem structure is critical for supporting increased grain biomass, while maintaining resistance to lodging.

The ideal wheat canopy exhibits a top-down gradient of leaf angles, with erect upper leaves enhancing light penetration to the lower-layer canopy, while more horizontal lower leaves would maximize light interception [18]. Flag leaves should be short, wide, thick, and dark green to efficiently facilitate photosynthesis and grain yield formation. Reduced tiller numbers with fewer unproductive tillers should enhance resource allocation to spikes, supporting the development of large spikes and grains with a high harvest index exceeding 0.62 [19]. Yield improvements have historically relied on increased grain numbers without compromising grain weight, making spike weight a promising target for future breeding and genetic engineering efforts [20]. A deep, well-developed root system enhances water and nutrient uptake, supporting aboveground growth and ensuring plant resilience under stressful conditions [21] (Figure 2B).

Maize

Long-term breeding has shown limited potential for further yield improvements in maize by increasing the ear size of individual plants. Under the constraints of limited arable land and low

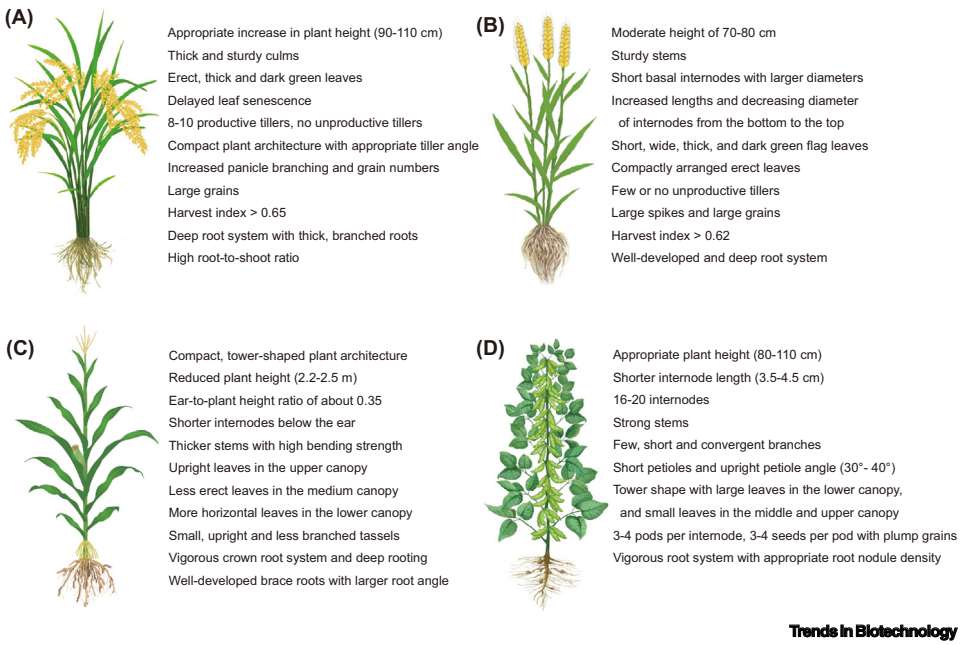

Figure 2. Ideal architectypes for rice, wheat, maize, and soybean. (A) Rice; (B) wheat; (C) maize; (D) soybean. Favorable traits that contribute to the ideal architectype are listed for each of the four crops.

nutrient utilization efficiency, dense planting has become the most effective strategy for increasing maize yields. Consequently, the ideal maize architectype should be compact and tower shaped, with upright leaves above the ear (leaf angle: 10°–18°) and high leaf orientation values [22]. A 'smart-canopy' architecture with upright leaves in the upper canopy, less erect leaves with increased length in the middle canopy, and horizontal leaves in the lower canopy minimizes shading, enhances ventilation, and improves light transmittance [23,24]. Functionally important leaves such as the ear leaf and those immediately above and below the ear should be nearly horizontal to maximize light capture and photosynthesis, with a leaf area index above 6.0 [25]. Compact **tassels** with fewer branches would reduce competition for resources with the ear and improve biomass allocation to kernels, while short **anthesis-silking intervals (ASI)** can enhance pollination and seed development under drought or high-density conditions [26].

Dense planting triggers shade avoidance responses (SAR) that lead to exaggerated stem elongation and reduced internode diameter, which together increase lodging risk. To mitigate these risks, the ideal maize plant should exhibit a height ranging from 2.2 to 2.5 m, which is shorter than most currently grown elite varieties, with an optimal ear-to-plant height ratio of 0.35–0.40, shorter internodes below the ear, and thicker stems with high bending strength to resist lodging [27]. A 'short-stature' maize variety recently introduced by seed companies enhances lodging resistance, **nitrogen-use efficiency (NUE)**, and compatibility with mechanical harvesting [28]. Additionally, a 'steep, cheap, and deep' root system, including vigorous crown roots and well-developed brace roots with steep angles, provides anchorage, supports water and nutrient uptake, and further improves lodging resistance [29]. All these traits will make maize more resilient and productive under dense planting conditions (Figure 2C).

Soybean

In contrast to the significant yield improvements in rice and wheat during the Green Revolution, soybean yields have stagnated, necessitating the development of new approaches in soybean

breeding. As a pod crop, soybean has some unique morphological features, with leaves, inflorescences, and pods growing at each node. This architecture limits the possibilities to achieve yield improvements through plant height reduction. Semi-dwarf soybean varieties with fewer internodes, unlike rice, wheat, and maize, are not effective in conferring substantial yield increases. Instead, optimizing the relationship between plant height and internode characteristics is essential. Taller soybean plants offer more internodes for fruit set, but are prone to lodging, whereas shorter plants resist lodging but have fewer internodes. Studies suggest an optimal plant height of 80–110 cm, a short internode length of 3.5–4.5 cm, and a total number of 16–20 internodes with strong stem diameter [30,31]. To maximize yields on the available arable land, increasing planting density will be key, which makes branch architecture a critical consideration. Under high-density planting conditions, soybeans with numerous, long branches would suffer from reduced light capture and also hinder growth of neighboring plants. Therefore, the ideal soybean architectype features few, short, and convergent branches with a strong main stem [32].

Additionally, large petiole angles and long petioles can cause self-shading, thus reducing light-harvesting efficiency and making the plants unsuitable for dense planting. Therefore, a short petiole with an upright angle of 30°–40° is strongly preferred [33]. An ideal canopy structure has large leaves in the lower canopy and smaller leaves in the middle and upper canopy, forming a tower-shaped spatial distribution [34]. Since soybean yield per plant largely depends on pod number rather than seed weight, three or four pods per internode and four plump seeds per pod are considered ideal for yield improvement [35]. Soybean roots form nodules with symbiotic diazotrophic *Rhizobium* bacteria, enabling biological nitrogen fixation, which is critical for plant growth and development. The ideal soybean ideotype should have a vigorous root system with robust root nodules, ensuring efficient nutrient uptake and translocation as well as stress resilience (Figure 2D).

Plasticity under high-density planting conditions

High-density planting is a critical strategy to improve agricultural productivity. In this context, crops with high plasticity – the ability to adjust growth and development in response to varying environmental factors – are crucial for optimizing yields and ensuring stability [36]. Ideal crops should exhibit specific architectural modifications such as reduced leaf angles and tiller numbers to minimize competition for light and resources, while maintaining plant height to prevent excessive shading and resource depletion, as planting density increases.

Rice, wheat, maize, and soybean display significant plasticity in response to planting density. Rice reduces tillering under high-density conditions and adapts its root architecture to water availability – forming shallow roots in flooded conditions and deeper roots in drought-prone environments [37]. Wheat adjusts tiller formation to ensure full canopy coverage ('ridge sealing'), thus optimizing light interception and suppressing weed growth [38]. Maize suppresses tiller formation under high density, focusing resources on a single dominant ear; whereas it produces additional tillers and secondary ears at low planting densities with adequate light and radiation conditions to enhance biomass and yield potential [39]. Soybean adjusts branching and pod-bearing habits, with infinite pod-bearing favoring long growth cycles and finite pod-bearing to short growth cycles or limited growth spaces [40].

Breeding for these adaptive traits is essential to develop new high-yielding varieties capable of thriving in high-density settings, while ensuring efficient resource utilization, to meet the demands of modern agriculture.

Optimal physiotype

The concept of the ideotype is dynamic in that it needs to continuously evolve by adjusting to changing climatic and environmental conditions as well as changing agronomic practices.

While plant morphology has traditionally been the primary focus of ideotype development, there is growing recognition that physiological traits are equally crucial for maximizing crop yields, as changes in physical structure alone do not directly alter physiological processes. For instance, modifying leaf angle can improve light utilization efficiency, but does not inherently enhance photosynthetic capacity. The integration of both architectural and physiological traits, with the latter referred to as the 'optimal **physiotype**' (i.e., the sum of the physiological characteristics of plants under specific environmental conditions), holds significant potential to maximize yields across diverse environments and resource availability constraints. An excellent example of such an approach is the release of IR8, the first semi-dwarf rice variety development by IRRI in 1966. IR8 featured a dwarf, compact morphology combined with enhanced physiological traits (e.g., high photosynthetic efficiency and robust grain-filling capacity). These combined features were responsible for IR8 conferring substantial yield increases, with grain yields being up to 2–3 times higher than those of traditional rice varieties [41]. Thus, developing crops with both ideal architectypes and optimal physiotypes is central to advancing the next Green Revolution.

High photosynthetic efficiency

As the green engine of life on Earth, photosynthesis converts the energy of the sunlight into chemical energy, thus enabling biomass production in nearly all ecosystems. However, the low energy conversion efficiency of photosynthesis (<1%) severely constrains crop yield improvement [42]. Climate change and, in particular, rising temperatures and CO_2 levels, further complicate efforts to optimize photosynthesis in crops through breeding efforts.

To address these challenges, several strategies have been explored to improve photosynthesis and boost crop productivity. One approach proposed is to expand the light spectrum available for photosynthesis by incorporating the capacity to utilize far-red light into the canopy, either through architectural modification of the canopy structure or by introducing far-red light-harvesting pigments [43]. Another strategy that has been pursued focuses on genetic engineering to optimize key photosynthetic pathways, for example, by accelerating nonphotochemical quenching kinetics to help crops cope with fluctuating light conditions [44]. Additionally, modifying electron transport processes within the thylakoid membrane can further improve yield potential. Other efforts aim to enhance the Calvin cycle by upregulating gene expression or improving enzyme efficiency, which can drive significant yield improvements [45]. Moreover, enhancing photosynthesis during the post-anthesis period by introducing traits like stay green and extended grain filling can maintain high photosynthetic efficiency and stabilize yields, particularly in challenging environments [8,46].

Efficient nutrient utilization

Nitrogen and phosphorus are essential nutrients for plant growth, and directly influence crop yields through their role in various physiological processes. However, excessive application of nitrogen and phosphorus fertilizers has led to pollution, especially eutrophication of freshwaters, and environmental degradation. In Green Revolution varieties (GRVs), NUE has often been compromised, particularly due to the accumulation of DELLA proteins, which are associated with the semi-dwarfism trait [4]. To address the challenge of improving NUE and phosphorus use efficiency (PUE) and reducing fertilizer inputs, it is essential to break the trade-off between plant growth and nutrient utilization to achieve a more sustainable food production.

Nutrient use efficiencies are complex traits involving processes such as uptake, transport, assimilation, and remobilization. Enhancing these processes could be achieved, for example, by modifying root architecture to improve nutrient uptake, including increasing root density, surface area, and plasticity [47]. Optimizing nutrient transport within the plant is also a key aspect, with current

efforts being focused on modifying the expression of nutrient transporters, such as NRTs for nitrate, AMTs for ammonium, and PHTs for phosphate [48,49]. Additionally, regulating metabolic enzymes like nitrate reductase and glutamine synthetase, and/or regulators of nutrient signaling (e.g., PHR1, SPX) can enhance assimilation efficiency [50,51]. Improving nitrogen remobilization to developing grains and enhancing phosphorus recycling from senescing organs also represent promising approaches to optimize nutrient allocation [52,53]. The identification of critical transcription factors such as the NGR5–DELLA–GRF4, OsTCP19–DLT, and PHR1–SPX modules [54], and the optimization of the carbon–nitrogen balance by modifying the associated metabolism [55], holds potential for improving NUE and PUE. In summary, by closing knowledge gaps and engineering factors involved in nutrient acquisition and remobilization, it should be possible to significantly enhance crop resource use efficiency.

Stress resilience

Extreme weather events, such as drought periods, floods, and heat waves, are becoming more frequent and intense due to climate change, and pose significant threats to global crop production. Enhancing crop resilience to these stresses will require the translation of molecular insights gained in model plants to staple crops and equip them with the capacity to withstand multiple stresses under field conditions. Feasible strategies include the use of advanced breeding techniques (including genome editing and transgenic methods) as well as improved management practices and the use of microbial consortia to enhance stress tolerance [56].

A resilient root system plays a key role in maximizing water capture and also enhances tolerance to adverse conditions. Optimizing root architecture and metabolic efficiency can help crops better adapt to extreme conditions [14,57]. Modifying stomatal traits, such as size, density, aperture, and movement dynamics, can optimize the balance between photosynthesis and stress tolerance, especially under water-limited conditions [58,59]. The regulation of stress-responsive hormones [e.g., abscisic acid (ABA), gibberellin (GA)] and stress-associated signaling pathways (e.g., calcium, MAPK, TOR, and SnRK signaling) offers another feasible strategy to coordinate growth with stress tolerance [60–62]. Improving resistance to extreme temperature conditions will be particularly important for crops in tropical and subtropical regions, where heat stress is a growing concern [63].

In addition to genetic improvements, agronomic management practices and soil microbiome engineering can also play important roles in enhancing stress resilience. Diversified cropping systems, including intercropping and crop rotation, that are tailored to local environmental conditions can promote root growth, optimize nutrient distribution, and enhance soil microbiome diversity, all of which are important factors that contribute to sustainable and environmentally friendly agricultural productivity [64]. For example, high-yielding rice cultivars have been shown to reduce CH_4 emissions from paddy soils [65]. Advanced technologies such as drones equipped with multispectral cameras are increasingly used for precise crop monitoring, enabling better field management and faster reaction to the changing needs of the crop in response to changing environmental conditions.

Coordination of physiological processes

Plants operate as integrated systems, where the coordination of multiple physiological processes, including photosynthesis, nutrient utilization, and stress responses, is essential for optimal growth and yield. These processes are highly interconnected, with improvements in one of them often impacting the others. For example, photosynthesis and nitrogen metabolism are tightly linked, as amino acid synthesis requires carbon skeletons derived from photosynthetic CO_2 fixation. Proteins involved in photosynthesis, such as the primary CO_2-fixing enzyme

Rubisco, not only catalyze carbon fixation, but due to their sheer abundance, also serve as major nitrogen reservoirs. Enhancing the efficiency of photosynthetic carbon fixation through genetic engineering and/or exploration of its natural diversity remains a high priority for improving photosynthesis and resource use efficiency, although this has proven to be a very challenging target [66,67]. Similarly, traits like stay green and extended grain filling can sustain photosynthetic activity and nutrient remobilization, and in this way, contribute to yield stability under stress conditions. Our understanding of the (highly complex) regulation of photosynthesis and nitrogen utilization is still incomplete, and the elucidation of the regulatory networks underlying the coordination of carbon and nitrogen metabolism will be essential to facilitate new engineering approaches [68].

The **water-use efficiency (WUE)** of crop plants is receiving increasing attention in breeding, as water scarcity becomes more severe in many regions of the world. Improved root architecture, dynamic stomatal regulation, and reduced nonstomatal water loss can potentially align photosynthesis with water conservation needs, while maintaining efficient nutrient uptake and stress tolerance. At the same time, energy efficiency and, in particular, the proper balancing of ATP and NADPH production with the demands of downstream metabolism support efficient photosynthetic carbon fixation, nutrient assimilation, and stress responses [69,70]. Proper temporal and spatial regulation of source–sink relations ensures effective allocation of carbon and nutrients to developing grains or storage organs, thus maximizing productivity while maintaining resilience [71,72].

Interactions of plant roots with soil microbes can also enhance nutrient uptake, affect stress resilience, and overall plant health. Incorporating beneficial microbial consortia into breeding and crop management strategies has significant potential and can complement plant-based improvements [64,73]. Also, addressing biotic stresses such as pests and diseases alongside abiotic challenges will be essential for obtaining a holistic picture that integrates all aspects that contribute to the ideal physiotype. Leveraging genomics, transcriptomics, and artificial intelligence (AI)-based tools to understand and manipulate these interconnected processes will enable the development of resilient, resource-efficient crop varieties that are adapted to climate change.

Multidisciplinary approaches for ideotype breeding

The domestication of crops by humans has spanned >10 000 years and is still ongoing. Modern crop breeding focuses on integrating desirable traits in domesticated plants, and leveraging the genetic diversity of traditional landraces and wild relatives. The development of new powerful computational tools, including meta-analyses, machine learning, Bayesian approaches, and artificial neural networks, combined with high-throughput phenotyping, genotyping, and multiomics analyses, will enable more precise genotype–phenotype mapping. This will facilitate gene and allele mining in large germplasm collections, thus greatly accelerating the identification of optimal trait combinations [74,75]. For example, haplotype-based genome-wide association studies enable the identification of beneficial trait combinations without the need for lengthy breeding cycles, and thus can bypass the time-consuming and labor-intensive traditional breeding methods based on crosses, back-crosses and large-scale evaluation of the progeny [76]. The application of genomic prediction techniques and the rapid identification of superior haplotype alleles can significantly accelerate the pace of crop improvement in the coming decades (Figure 3).

Advanced genome editing technologies such as clustered regularly interspaced short palindromic repeats (CRISPR)-CRISPR-associated protein (Cas) (including precision gene editing techniques such as base editing and prime editing) enable targeted and more precise genomic

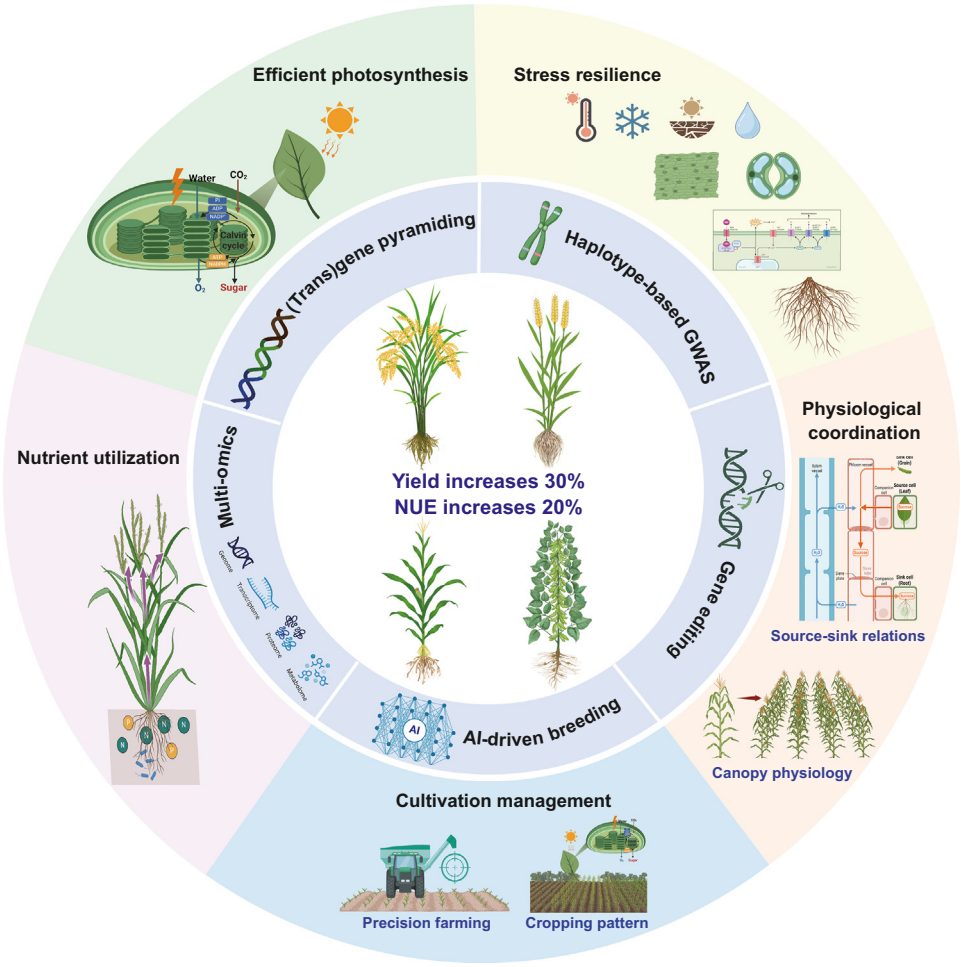

Figure 3. Schematic representation of key factors contributing to the next Green Revolution. New crop varieties that are based on integrating the ideal architectype with the optimal physiotype form the foundation of the next Green Revolution. The optimal coordination of carbon and nitrogen metabolism, optimized source–sink relations, and an intelligently engineered canopy structure, combined with improved photosynthetic efficiency, high nutrient use efficiency, and stress resilience, will be key features of the crops of the future. Harnessing the full potential (and the synergies) of these approaches is expected to boost average crop yields and nutrient use efficiency by over 30% and 20%, respectively, making a significant contribution to global food security and the increased sustainability of agricultural production systems. Abbreviations: AI, artificial intelligence; GWAS, genome-wide association study; NUE, nutrient-use efficiency. Figure created with BioRender.com.

manipulations and are already revolutionizing crop breeding [71,77]. These new tools, combined with spatially and temporally resolved omics analyses and systems biology approaches, are providing unprecedented insights into the regulatory mechanisms that govern complex physiological processes in plants. A particularly promising strategy facilitated by these developments involves the discovering, creating, and stacking of multiple beneficial genes, a process also referred to as 'physiological pyramiding', which aims to combine desirable traits into a single crop variety. Genome editing tools and their unparalleled capacity for multiplexing will speed up this process enormously. Integration of these precision breeding approaches with innovative farming systems such as crop rotation, intercropping, and precision irrigation can enhance nutrient use efficiency and, at the same time, mitigate the effects of environmental stresses. A study in Nebraska, USA (2005–2018), concluded that agronomic management contributed 39% to yield gains, whereas

the contribution of genetic improvements was only 13% [78], underscoring the importance of integrating breeding and genetic engineering efforts with optimized management practices (Figure 3).

The ideal crop varieties of the future should require fewer resources, including water, fertilizers, pesticides, herbicides, labor, and land, while also promoting the sustainable intensification of agricultural production systems. Smart breeding strategies, using a combination of elite genes and alleles, AI-assisted genomic prediction tools, and directed evolution, together with a synthetic biology approach, show promise for the rational design of crop varieties that can meet current and future challenges in crop production (Figure 3). As ideotype breeding extends from individual plants to canopy-level cropping systems, interdisciplinary and systems-based approaches will be crucial to address the complexity of the genetic and environmental factors involved in determining crop yield and yield stability under changing environmental conditions.

Concluding remarks and future perspectives

Arguably, the first Green Revolution was one of the pivotal milestones in agricultural history, as it revolutionized crop productivity and modernized agronomic practices. However, as the global population approaches 10 billion, the dual challenges of dwindling natural resources and escalating environmental stresses demand innovative solutions to ensure sustainable food security. In this Review, we have highlighted the critical need to develop crop varieties with optimal physiotypes that complement ideal architectural traits as the cornerstone of a new Green Revolution. Key priorities include the coordination of carbon and nitrogen metabolism, optimization of source–sink relationships, and enhancement of both individual plant and canopy-level performance. Traits such as the ability to automatically adjust the optimal tiller or branch numbers to the growth conditions, a robust and plastic root system adaptable to varying conditions, efficient photosynthesis, high nutrient use efficiency, and enhanced stress resilience, should be prioritized and will be indispensable for future crops in the next Green Revolution. Precise control of plant hormones, such as GA, BR, and strigolactone, represents a promising avenue for optimizing plant architectype and/or physiotype, as demonstrated by many recent studies [12,23,61,79,80]. Traits enabling efficient photosynthesis and high performance under high-density planting conditions will be pivotal, as they address the primary limitations that currently hinder yield improvement in major crops, akin to the transformative impact of semi-dwarf traits during the first Green Revolution. Synergizing these advancements is projected to increase average yield and nutrient-use efficiency by over 30% and 20%, respectively (Figure 3).

To realize this vision, systems biology approaches powered by AI, machine learning, and high-throughput phenotyping, provide a robust framework for germplasm exploration and the systematic identification of genes and allelic variation underlying complex quantitative traits (Box 2). Developing a comprehensive crop gene resource bank database that integrates genotypic and phenotypic data – encompassing architectural and physiological traits – from diverse germplasms will further accelerate the discovery and deployment of beneficial traits. In this context, it is imperative to initiate the **Crop Pan-Genome Decoding Project** and the **Crop Phenome Project**. This, in turn, will facilitate the development of AI-driven smart crop breeding platforms. The integration of these advanced tools with cutting-edge genetic engineering technologies, holds immense potential to expedite the development of crop varieties with tailored traits. In combination with precision agronomic practices, these innovations may herald the dawn of a new agricultural revolution, ensuring sustainable productivity in the face of global challenges (see Outstanding questions).

Outstanding questions

What constitutes the ideal architectype for specific climatic zones and environmental conditions?

What are the regulatory mechanisms that link architectype and physiotype, and how do they need to be modified to maximize crop performance?

How can the integration of ideal architectype and optimal physiotype occur most efficiently in crop breeding?

What roles can emerging technologies such as artificial intelligence and synthetic biology play in enabling the next Green Revolution?

Box 2. The role of AI and synthetic biology in the next Green Revolution

Together with rapid advancements in computational and genomic technologies, AI and synthetic biology are transforming agriculture by addressing critical global challenges, including climate change, population growth, and resource constraints. AI-driven high-throughput phenotyping, powered by drones and imaging sensors, enables real-time plant growth and stress response monitoring. For example, LemnaTec's PhenoAIxpert automates field phenotyping, while AI-powered tools such as the ICRISAT-Microsoft's AI Sowing App and Penn State University's PlantVillage app enhance weed identification and disease detection. Field management platforms like IRRI's Rice Crop Manager, the Africa Rice Center's RiceAdvice, and Bayer's FieldView optimize planting schedules, monitor crop health, and improve irrigation strategies and yield forecasting, thus enabling data-driven decision-making to enhance resource efficiency and productivity.

AI and machine learning algorithms analyze large-scale genomic datasets to help identify key traits associated with yield improvement, stress tolerance, and pest resistance. By deciphering genotype-to-phenotype relationships, AI models can pinpoint genes controlling complex agronomic traits such as drought resilience and nutrient uptake. AI-powered breeding platforms, including Bayer's Precision Breeding platform and IRRI's Global AI-Hybrid Rice Platform, optimize parent selection and predict hybrid performance, thus significantly accelerating breeding cycles across diverse environmental conditions

Synthetic biology complements AI by engineering biological systems to enhance crop performance. Initiatives such as Realizing Increased Photosynthetic Efficiency, C_4 Rice, and Gains4Crops focus on improving photosynthetic efficiency, while the engineering of root-associated microbial consortia is pursued to enhance nitrogen-use efficiency. Biofortification efforts such as Golden Rice address nutritional deficiencies, and *de novo* domestication strategies facilitate the development of novel crop varieties with customized agronomic traits. AI plays a crucial role in these efforts by identifying genome editing targets and, in this way, enabling precise modifications of biological pathways to maximize yield potential.

Despite these advancements, several challenges remain. Many agronomically important genes have yet to be fully characterized, and complex genetic interactions and pleiotropic effects complicate trait engineering. Integrating multiomics datasets with AI models requires high-quality environmental and biological data to enhance prediction accuracy. Validating AI-driven insights at the field scale presents further technical and logistical hurdles. Overcoming these challenges will strengthen the predictive power and real-world applicability of AI and synthetic biology approaches in agriculture.

Together, AI and synthetic biology will very likely drive the next Green Revolution, accelerating agricultural innovation and bolstering global food security.

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Declaration of interests

The authors declare no competing interests.

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