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Perspective

Toward Ratoon Biology of whole-plant regeneration across seasons

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ABSTRACT

Ratoon-based cropping systems have re-emerged as a strategy to enhance productivity and resource use efficiency in crop production; however, the mechanisms governing regeneration across harvest cycles remain poorly understood, resulting in highly variable and unpredictable performance. Ratoon yield depends on two tightly coupled components: the establishment of reproductive tillers that form yield-bearing units and the productivity of each unit, which were determined by organ differentiation and biomass accumulation. Here, we propose Ratoon Biology as a conceptual framework that redefines ratooning as a continuous, whole-plant developmental process that extends across seasons. We identify five interacting dimensions that jointly regulate ratoon productivity. First, ratoon buds determine regenerative potential through their meristem viability, dormancy status, and competitive competence. Second, stubble functions provide the structural and metabolic foundation for regeneration by maintaining vascular continuity, supplying carbon and nitrogen reserves, and integrating systemic signals. Third, root–shoot coordination enables the rapid re-establishment of hydraulic, nutritional, and hormonal coupling between residual roots and emerging shoots, thereby supporting early tiller vigor. Fourth, tiller regeneration and establishment represent a selective developmental process shaped by nodal competition, spatial heterogeneity, and unequal access to internal resources, together determining which buds survive to become productive tillers. Fifth, inter-seasonal continuity reflects the developmental and physiological legacy linking the main crop to subsequent ratoon performance through structural, metabolic, and regulatory carry-over effects, including persistent plant–microbe interactions. By framing ratooning as an integrated, cross-seasonal biological system, Ratoon Biology establishes a roadmap for future research that targets key mechanistic gaps and provides a conceptual basis for next-generation breeding and management strategies aimed at improving multi-season productivity.

1. Introduction

Over the past decade, ratoon-based cropping systems have undergone a remarkable resurgence (Peng et al., 2023; Wang et al., 2019). Driven by the imperatives for sustainable intensification, improved resource use efficiency, and reduction in labor input, ratooning has shifted from a marginal agronomic practice to a central research focus in crop science and an increasingly important paradigm in global crop production (Lin, 2019; Xu et al., 2021). This transition is evident across major staple crops. In rice, ratooning has progressed from localized experimentation to widespread adoption and intensive investigation across Asia, where it is valued for enhancing annual productivity without expanding cultivated land (Peng et al., 2023). In sugarcane, ratooning represents the archetypal multi-season cropping system, forming the structural foundation of commercial production in tropical regions (Dlamini et al., 2024). Similarly, ratoon sorghum provides a resilient and mechanization-friendly model for intensifying production in moisture-limited environments and optimizing the balance between biomass accumulation and resource conservation (Zhou et al., 2021). More recently, the development of perennial rice has further extended the conceptual boundaries of cropping systems (Zhang et al., 2023b), demonstrating the feasibility of sustained multi-season productivity from a single planting event.

Despite this growing prominence, research on ratoon systems has remained largely empirical. Most studies have focused on optimizing management practices such as harvest timing, cutting height, irrigation, fertilization regimes, and pest control (Lin, 2019; Nakano et al., 2023; Wang et al., 2019; Xu et al., 2021). These efforts have led to substantial improvements in system viability and yield stability. However, the incremental gains achieved through agronomic refinement are increasingly approaching a performance ceiling, suggesting that further advances are unlikely to arise from management optimization alone (Lin, 2019). Progress has been constrained by a limited understanding of the biological processes that govern regeneration, with key components of ratoon performance still evaluated primarily through field-level outcomes rather than mechanistic integration (Lin, 2019; Yao et al., 2023).

Across crops and production contexts (Fig. 1), ratooning consistently depends on the ability of harvested plants to regenerate from residual vegetative tissues, particularly axillary buds, allowing growth to resume without replanting (He et al., 2019; Xu et al., 2021). This shared biological dependence reveals a fundamental commonality that transcends crop-specific practices and challenges conventional views of crop

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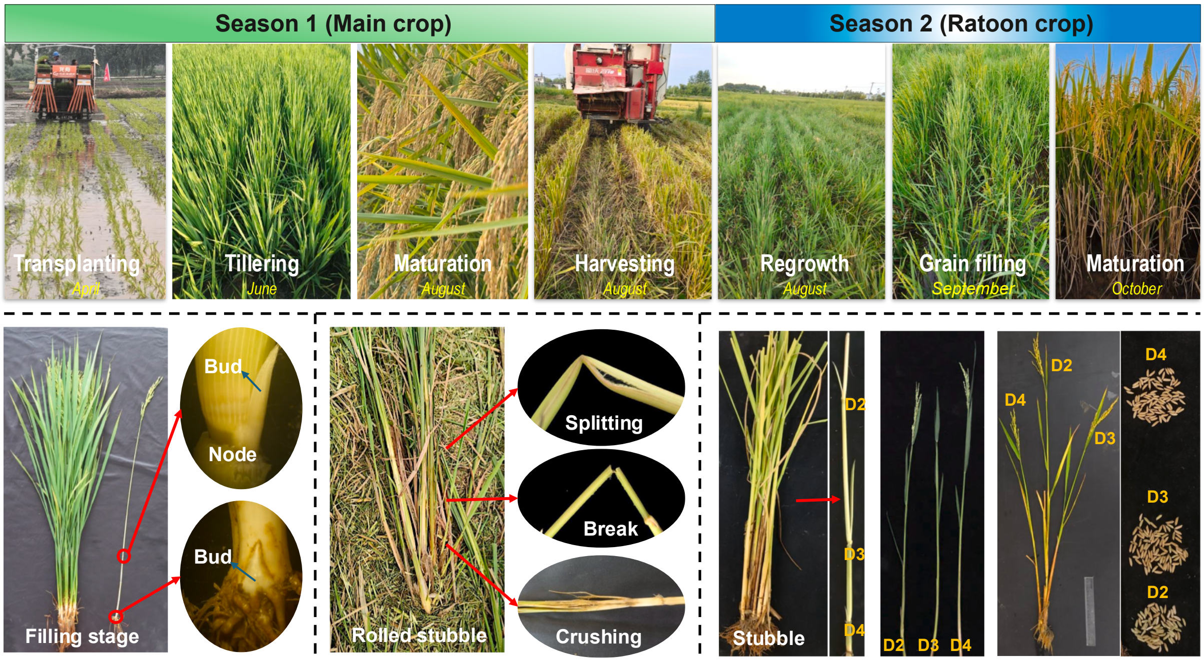

Fig. 1. Representative images illustrating the inter-seasonal continuity, regenerative foundations, and yield formation of a mechanized ratoon rice system. Panels are separated by dashed lines. Top row shows the seasonal progression of the ratooning cycle, from the main crop (Season 1) to the ratoon crop (Season 2). The main crop undergoes transplanting, tillering, and maturation, followed by mechanical harvesting, while ratoon regeneration initiates immediately after harvest and proceeds through rapid regrowth, grain filling, and final maturation. The months indicated represent a typical ratoon rice production schedule under prevailing management practices in Hubei Province, China. Bottom left panels show the development of axillary buds at the grain filling stage of the main crop. Bottom middle panels illustrate typical mechanical damage to stubble caused by mechanized harvesting. Such damage disrupts vascular continuity and compromises bud-root connectivity, providing a mechanistic explanation for regeneration failure in mechanically harvested ratoon systems. Bottom right panels show variation in regenerated tiller emergence, panicle development, and final grain yield. D2, D3, and D4 denote regenerated tillers originating from 2nd, 3rd, and 4th nodes counted from the top of the stubble, respectively.

production as a sequence of isolated growth cycles. Instead, ratooning reflects a biologically continuous process that links developmental events before and after harvest (Hu et al., 2024; Huang et al., 2022). However, the mechanisms that enable this continuity remain poorly understood. Core processes such as bud dormancy breaking, hormonal regulation, carbohydrate remobilization, and root system renewal are often examined in isolation, obscuring their coordinated roles within the whole plant (Gai et al., 2025; Hu et al., 2025; Xie et al., 2025; Xu et al., 2020). As a result, ratoon performance is frequently interpreted as the stochastic outcome of management and environmental interactions rather than as the emergent behavior of an integrated biological system (Nie et al., 2025). Addressing this gap requires a conceptual reorientation from viewing ratooning as a reactive post-harvest response to understanding it as a proactive and developmentally continuous process. Therefore, there is a need to articulate a cohesive framework for Ratoon Biology that captures the temporal continuity, functional complexity, and systemic integration inherent to regenerative cropping and elevates ratoon agriculture from a collection of crop-specific practices to a unified field of biological inquiry.

2. Defining Ratoon Biology

We propose defining Ratoon Biology as the study of plant regeneration conceived as a continuous, cross-seasonal developmental process. Within this framework, harvest of the main crop is understood neither as an origin nor as a terminus, but as a pivotal biological transition (Fig. 2). It marks the point at which developmental momentum, which is shaped by earlier processes such as bud establishment, resource storage, and root system architecture, intersects with the abrupt physiological reprogramming triggered by canopy removal (Fig. 1).

Adopting a continuum-based perspective necessitates a re-evaluation of the temporal boundaries traditionally used to demarcate crop development. During the main crop phase, the plant undertakes two interdependent functions. It not only accumulates yield for the current season, but also constructs the regenerative infrastructure, including competent buds and viable stubble, that underpins subsequent ratoon emergence. Regenerative capacity, therefore, is not abruptly induced by cutting; rather, it is progressively encoded throughout the plant's developmental trajectory (Hu et al., 2024). The ratoon phase itself is likewise not a discrete growth cycle. Instead, it represents the expression of inherited regenerative continuity. Regrowth unfolds within a complex internal milieu defined by a mature yet decapitated vascular system, a persistent root network, and reconfigured hormonal dynamics (Nakano et al., 2021; Nie et al., 2025). Successful regeneration depends on the plant's ability to reorganize these residual structures into a coherent and functional vegetative system.

From a yield-oriented perspective, the central task of Ratoon Biology is to elucidate the biological basis of ratoon productivity (Fig. 2). This productivity is determined by two tightly coupled components. The first is the proportion of regenerated buds that successfully develop into reproductive tillers and form yield-bearing units, which can be viewed as the efficiency of tiller establishment. The second is the productivity of each unit, which is determined by organ differentiation and biomass accumulation. In cereal crops, these correspond to productive panicle number and yield per panicle, respectively. Ratoon yield therefore does not arise simply from bud survival or from resource availability alone, but emerges from the coordinated regulation of regenerative success and reproductive performance at the level of individual tillers. This perspective places Ratoon Biology at the interface between regeneration biology and yield biology, emphasizing that yield formation is inseparable from developmental selection during regrowth. It requires an integrated understanding of how bud competence, stubble metabolic and vascular function, root-shoot coordination, and inter-seasonal continuity jointly govern both the establishment of reproductive units and the capacity of each unit to express its yield potential. In this sense, these dimensions frame ratooning not as a discrete post-harvest response, but as a temporally integrated process of whole-plant regeneration in which regeneration, internal competition, and yield formation are biologically inseparable (Fig. 2).

3. Core dimensions of Ratoon Biology

3.1. Ratoon buds

Axillary buds located at stubble nodes constitute the essential biological foundation of ratoon cropping (Xu et al., 2021). Accordingly, Ratoon Biology is fundamentally concerned with the life history of these regenerative meristems, from their initiation and maintenance during the main crop phase, through their reactivation after harvest, to their functional integration with the residual stubble, root system, and surrounding environment. In the absence of viable and developmentally competent buds, ratoon regeneration fails, even under otherwise favorable agronomic conditions (Yu et al., 2022).

The regenerative potential of a bud is established well in advance of harvest (Fig. 1). During main crop development, axillary meristems are initiated and potentially enter a state of paradormancy under the influence of apical dominance (Nakano et al., 2021). This dormancy is not merely passive; rather, it reflects a dynamic regulatory equilibrium that suppresses premature competition with the dominant reproductive axis. Under certain physiological conditions, such as damage to the primary panicles or elevated nitrogen availability, this balance may be disrupted, leading to early bud activation in rice (He et al., 2023). Such precocious outgrowth often occurs during grain filling and is generally regarded as agronomically undesirable.

Harvest acts as a major biological trigger in the ratoon system (Chen et al., 2023). Removal of the canopy and the apical sink profoundly alters internal signaling networks, thereby releasing inhibitory constraints on nodal buds. To exploit this window of opportunity, buds must rapidly transition from dormancy to active growth, initiating cell division and organogenic programs. This dormancy-to-activation shift represents a critical developmental bottleneck in the establishment of a ratoon crop. Despite its central importance, the molecular and physiological mechanisms governing this transition remain incompletely understood (Yao et al., 2023). Although phytohormones such as auxin, cytokinins, and strigolactones are widely presumed to coordinate dormancy breaking, the specific regulatory networks operating within ratoon systems have yet to be systematically elucidated (Hu et al., 2025; Xu et al., 2020; Yao et al., 2023).

Current evidence indicates that bud dormancy breaking in ratoon systems does not depend on any single regulatory factor. Instead, it emerges from coordinated interactions among carbon reserves, nitrogen availability, and phytohormonal signaling (Fig. 3). The accumulation of nonstructural carbohydrates in the stubble during the main crop season provides the principal energetic and metabolic support for early bud outgrowth in rice (Chen et al., 2022; He et al., 2023). The abundance of these reserves is strongly influenced by the source-sink relationships established during grain filling of rice (He et al., 2019). At the same time, plant nitrogen status affects both nonstructural carbohydrate accumulation and the sensitivity of buds to hormonal signals, thereby shaping their regenerative responsiveness (Hu et al., 2025; Xie et al., 2024). An elevated supply of cytokinin from residual root systems promotes bud activation, whereas auxin and strigolactone signaling impose positional dominance and competitive constraints (Zou et al., 2024). Increasing evidence further suggests that carbohydrate availability itself can modulate hormonal pathways by altering bud sensitivity to cytokinin and auxin (Hu et al., 2025). Through this coupling, metabolic status becomes directly linked to developmental control. Bud dormancy breaking should therefore be viewed as an integrative physiological

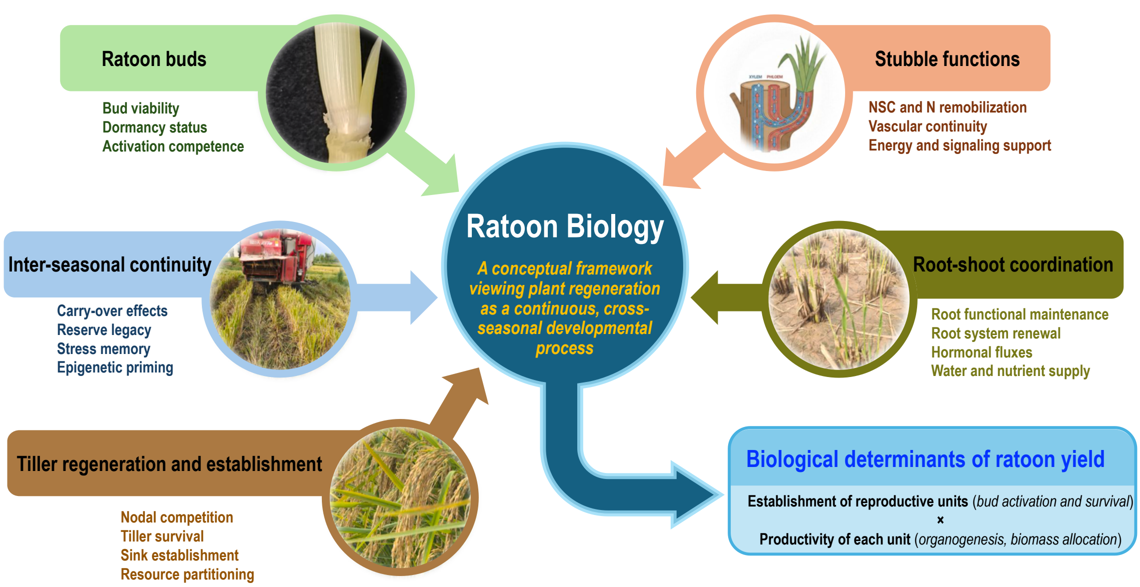

Fig. 2. Conceptual framework of Ratoon Biology illustrated as an integrated, whole-plant system in which regeneration and yield formation are biologically linked across seasons. Five interacting dimensions jointly regulate ratoon performance: (1) Ratoon buds define regenerative potential through bud viability, dormancy status, and activation competence; (2) Stubble functions provide metabolic and structural support via nonstructural carbohydrate (NSC) and nitrogen (N) remobilization, maintenance of vascular continuity, and the supply of energy and regulatory signals for early regrowth; (3) Root-shoot coordination integrates residual root function with shoot regeneration through root functional maintenance, new root turnover, hormonal fluxes (e.g. cytokinins, auxin, and ABA), and water and nutrient supply; (4) Tiller regeneration and establishment represent a selective developmental process in which regeneration is translated into reproductive structure formation through nodal competition, tiller survival, early sink establishment, and differential resource partitioning; and (5) Inter-seasonal continuity reflects the biological legacy linking the main crop to the ratoon crop, including carry-over effects, reserve legacy, stress memory, and epigenetic priming. Together, these dimensions define the biological determinants of ratoon yield, which can be resolved into two core components: the establishment of reproductive units through successful tiller formation and survival, and the productivity of each unit as determined by organ differentiation and biomass accumulation. In cereal crops, the two components correspond to productive panicle number and yield per panicle, respectively, with the latter governed by spikelet formation and the efficiency of grain filling.

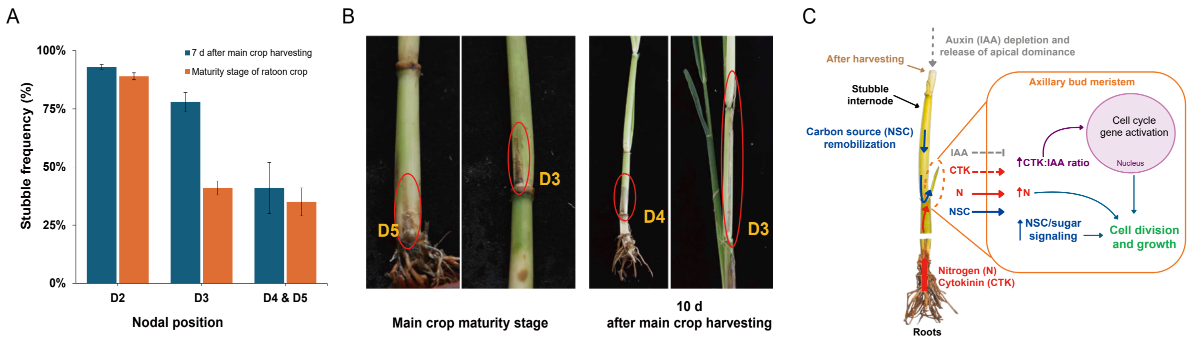

Fig. 3. Node-specific regenerated tiller survival and mortality in ratoon yield formation. (A) Frequency of stubbles exhibiting ratoon buds shortly after harvest or productive tillers at maturity at different nodal positions. D2-D5 denote nodal positions counted from the top of the stubble. Field investigations were conducted in 2023 at the experimental paddy field of Huazhong Agricultural University using the rice cultivar Liangyou 6326. All stubbles within 1 m^2 were surveyed. Values represent means ± SD (n = 3). (B) Representative images illustrating dead axillary buds at different nodal positions (D3–D5) observed at the main crop maturity stage (left) and 10 d after main crop harvest (right). (C) Schematic illustration of the physiological and molecular mechanisms by which stubble promotes axillary bud outgrowth after harvest. Removal of the auxin (IAA) source following harvest leads to the release of apical dominance, thereby enabling axillary bud activation. The stubble acts as both a reservoir and a transport conduit for the remobilization of non-structural carbohydrates (NSC) and nitrogen (N) and facilitates the upward transport of cytokinins (CTK) from the root system. These processes increase the CTK:IAA ratio in axillary buds, enhance N availability, and strengthen NSC and sugar signaling, which together activate cell cycle-related genes in the axillary bud meristem, ultimately promoting cell division, bud outgrowth, and tiller regeneration and establishment.

decision point at which stubble resource availability and systemic hormonal signaling jointly determine whether axillary meristems transition into actively regenerated tillers.

3.2. Stubble functions

While bud competence defines the potential for regeneration, its realization depends on the structural and physiological context provided by the old stubble. Within the framework of Ratoon Biology, stubble is best understood not as a passive remnant of the main crop but as an active interface that supports early ratoon development (Xu et al., 2021). Functionally, the stubble maintains vascular continuity between basal buds and the root system, enabling the transport of water, nutrients, and signaling molecules during early regrowth (Xie et al., 2025; Yuan et al., 2024). Mechanical damage incurred during harvest can disrupt this continuity, and the frequent failure of bud activation under such conditions underscores the essential role of the stubble in regeneration (Zhang et al., 2023a; Zou et al., 2024).

While bud dormancy breaking represents a developmental decision within the axillary meristem, its realization is contingent upon the structural and metabolic environment provided by the stubble. In the immediate post-harvest phase, before new leaves restore photosynthetic capacity, bud outgrowth relies largely on nonstructural carbohydrates, nitrogen, and other reserves stored in the stubble (Lal et al., 2023; Nakano et al., 2022). Mobilization of these reserves must occur while the stubble sustains its own respiratory demands, creating a balance that directly constrains the rate and success of bud growth. In addition to transportation and storage of reserves, the stubble likely integrates systemic and local signals, including root-derived hormonal cues and water status, thereby influencing the timing and spatial pattern of bud activation (Nie et al., 2025). The importance of stubble function is particularly evident in mechanically harvested ratoon rice systems, where cutting height, cutting uniformity, and mechanical disturbance directly shape stubble integrity (Fig. 1). Compared with manual harvesting, mechanical harvesting often increases variability in stubble structure and vascular continuity, amplifying the sensitivity of regeneration to stubble-mediated constraints (Peng et al., 2023). Despite clear functional evidence, the mechanisms underlying stubble-mediated regeneration remain poorly understood. How vascular integrity, reserve remobilization, and signal integration are coordinated to determine bud fate is still unclear, highlighting the need for a more mechanistic and integrative perspective on the regenerative roles of residual structures in ratoon systems.

3.3. Root–shoot coordination

Ratoon regeneration is fundamentally a whole-plant process that depends on the rapid re-establishment of functional coordination between shoots and roots (Nie et al., 2025; Xu et al., 2021). Although bud activation and stubble support are necessary, regeneration ultimately hinges on the ability of the root-shoot system to restore hydraulic, hormonal, and metabolic integration following harvest. At harvest, the root system typically enters senescence as a result of ontogenetic progression and extensive resource remobilization to the harvested organs. Root metabolic activity, hydraulic conductance, and structural integrity are therefore already in decline (Zhang et al., 2009). However, this aging root system is immediately required to undergo a functional reversal, supplying water, nutrients, and regulatory signals to emerging regenerated tillers. Residual roots must simultaneously sustain their uptake and signaling functions, providing cytokinins that promote bud activation while transmitting stress-related cues such as abscisic acid under hydraulic limitation (Hu et al., 2025). The capacity of senescing roots to transiently maintain these dual roles represents a key form of developmental plasticity that strongly influences early ratoon vigor.

Dependence on residual roots is brief but decisive. Before new nodal roots are established, pre-existing roots constitute the sole physiological connection between soil and shoot (Yuan et al., 2024). As regenerated tillers expand, shoot demand increases rapidly, and continued regeneration requires timely root system turnover (Deng et al., 2025). When new root initiation lags behind shoot expansion, hormonal feedback from stressed roots can restrict shoot growth, leading to tiller abortion. In this context, regeneration failure reflects not only a limited resource supply, but also a breakdown in coordinated root-shoot signaling. Successful ratooning therefore depends less on root biomass than on temporal synchrony. The decline of old roots and the establishment of new ones must be closely aligned with canopy redevelopment. Viewing root-shoot coordination as a central component of Ratoon Biology emphasizes regeneration as a systemic reconfiguration rather than a localized post-harvest response.

3.4. Tiller regeneration and establishment

In contrast to the main crop, which follows a relatively predictable sequence of vegetative and reproductive development, ratoon growth unfolds along a compressed and strongly condition-dependent trajectory (Shiraki et al., 2025; Yang et al., 2021). Ratoon yield potential is therefore governed by the absolute number of axillary buds retained on the stubble and by the proportion of these buds that survive, establish as tillers, and ultimately enter reproductive development (Nie et al., 2025). Although the total bud number on the stubble often exceeds agronomic demand, the final yield is the cumulative outcome of heterogeneous nodal contributions, each shaped by distinct physiological priorities and competitive strengths (Chen et al., 2023).

A defining feature of ratoon development is the rapid transition toward reproductive commitment, a process that is spatially heterogeneous along the stubble (Chen et al., 2023; He et al., 2023). Buds vary widely in their probability of establishment, indicating pronounced spatial heterogeneity along the stubble. This heterogeneity arises from positional differences in access to stored reserves, vascular connectivity, and hormonal signaling. As a result, tiller regeneration and establishment is inherently competitive, with buds at different nodal positions engaging in asymmetric interactions for limited resources and developmental precedence.

Upper-node buds such as D2 and D3 (regenerated buds in 2nd and 3rd node positions from the top of stubble, respectively) typically initiate growth earlier but often produce relatively small panicles, reflecting their proximity to residual stem reserves and rapid depletion of local resources (Fig. 1). In contrast, lower-node buds such as D4, and in some cases D5 (regenerated buds in 4th and 5th node positions from the top of stubble, respectively), maintain a more direct connection to the persistent root system, which supports sustained growth but is frequently associated with delayed emergence (Yu et al., 2022). This spatial heterogeneity intensifies intra-plant competition during early regrowth and results in substantial bud attrition. Recent evidence has identified intermediate nodes, particularly D3, as a critical failure point in high-stubble ratoon yield formation (Fig. 3). When both the reserve-favored D2 bud and the root-proximal D4 bud are simultaneously active, the D3 bud is often competitively suppressed, leading to elevated mortality. Despite its apparent importance, this sandwich effect and the underlying physiological mechanisms governing inter-nodal competition have received limited attention.

The characteristics of narrow temporal window of ratoon development further amplifies the effects of early competitive interactions. Short-term perturbations, including mild water deficits, insufficient stubble reserves, or delayed root turnover, can irreversibly constrain tiller establishment by destabilizing nodal hierarchies (Lan et al., 2026; Zheng et al., 2022). Under seasonal conditions marked by declining temperature and radiation, this selective pressure becomes more pronounced, favoring genotypes and management practices that promote rapid and coordinated establishment across multiple nodal positions (Hu et al., 2024; Xie et al., 2025).

Tiller regeneration and establishment should therefore be understood not as a uniform regeneration process but as a spatially structured developmental selection system operating within the stubble architecture. Final productive tiller number emerges from the outcome of nodal competition, in which developmental timing, resource accessibility, and hormonal signaling jointly determine which buds persist to contribute to yield (He et al., 2024; Huang et al., 2022). This perspective shifts the emphasis away from bud activation alone toward the regulation of bud survival and hierarchy, underscoring that the biological efficiency of ratoon systems depends on how effectively plants manage internal competition during the earliest phases of regeneration.

3.5. Inter-seasonal continuity

Plant development in ratoon systems is not reset by harvest but instead carries forward a legacy that links the main crop to subsequent regeneration. Developmental, physiological, and ecological imprints established during the main crop phase shape the trajectory of the ratoon crop, dissolving conventional temporal boundaries between production cycles (Nie et al., 2025). Structural features such as stubble integrity and vascular connectivity, physiological reserves retained in stems and roots, and the dormancy status of axillary buds are inherited from the preceding season and collectively define the biological context within which regeneration occurs (Lal et al., 2023; Xie et al., 2025).

Harvest does not erase this legacy but reveals it (Huang et al., 2022). Regenerative capacity following cutting reflects the cumulative influence of prior environmental conditions and management decisions. Stresses experienced during the main crop, including drought, nutrient limitation, or altered hormonal balance, can leave persistent molecular imprints such as metabolic reprogramming or epigenetic modification that continue to shape regenerative responses (Hu et al., 2024; Zheng et al., 2022). These carry-over effects help explain why similar post-harvest interventions often result in divergent ratoon outcomes depending on pre-harvest history (Huang et al., 2022).

Inter-seasonal continuity also provides a conceptual bridge between annual and perennial cropping strategies (Henry, 2024; Saito et al., 2024). By retaining living tissues across harvest events, ratoon systems reuse established developmental infrastructure and reduce the energetic costs of re-establishment, sharing functional similarities with perennial crops (Yuan et al., 2019). Recognizing this continuity situates regeneration within an explicitly temporal framework and underscores that ratoon performance emerges from linked biological processes operating across seasons rather than from post-harvest factors alone.

Beyond plant-intrinsic physiological and epigenetic mechanisms, plant-associated microbial communities and plant–microbe interactions may also play a role in sustaining harvest legacies across growing seasons (Zou et al., 2025). Main crop season environmental conditions and management regimes can shape rhizosphere and endophytic microbiomes, which may subsequently affect nutrient availability, hormonal signaling, and the stress tolerance of regenerating tissues. These microbially mediated influences can extend beyond the harvest event itself, interacting with host regulatory pathways to shape regrowth dynamics and thereby contributing to observed variation in ratoon performance even under comparable post harvest conditions.

4. Future perspectives

Here, we propose the establishment of Ratoon Biology as a coherent framework that highlights both conceptual progress and persistent gaps in mechanistic understanding. Although key processes such as bud activation, stubble function, root rejuvenation, and ratoon yield responses to environmental factors have been described, they are still largely investigated as isolated traits rather than as interacting components of a temporally continuous, whole-plant system. Importantly, the role of internal competition among regenerating organs has rarely been incorporated into these analyses. However, as emphasized throughout this review, ratoon performance emerges not only from the activation of regenerative structures but also from the plant's capacity to coordinate and resolve competition among buds, tillers, and roots under severe temporal and spatial resource constraints. Advancing the field of Ratoon Biology now requires addressing a set of foundational questions that define the limits of current knowledge (Nie et al., 2025).

A central unresolved issue is how to define a competent bud. While regenerative potential is widely thought to be determined during the main crop phase, no molecular or physiological criteria currently exist to distinguish dormant but viable buds from senescent or non-responsive ones prior to harvest. Moreover, competence should not be viewed solely as an intrinsic property of individual buds, but also as a relative trait expressed within a competitive context. Bud fate is ultimately determined by its ability to acquire resources and developmental priority in competition with neighboring nodes. Emerging approaches such as single-cell transcriptomics and spatial metabolomics provide promising avenues for identifying early markers of regenerative capacity and for developing predictive assessments of ratoon potential (Rich-Griffin et al., 2020; Seyfferth et al., 2021; Yin et al., 2024).

A second major uncertainty lies in identifying failure points within the stubble. As both a vascular conduit and a metabolic reservoir, the stubble occupies a critical position in regeneration, yet it remains unclear whether regeneration failure is primarily driven by impaired transport, carbon limitation, or their interaction (Sperry and Love, 2015; van den Ende, 2014). From the perspective of competition, stubble function also governs how resources are partitioned among competing buds and emerging tillers. Experimental approaches that disentangle resource availability from transport capacity would therefore be valuable not only for resolving this mechanistic uncertainty but also for clarifying how stubble mediated processes shape nodal dominance and competitive exclusion during early ratoon establishment.

Root system dynamics represent a further frontier. Ratoon regeneration requires aging roots to transiently reverse senescence and resume uptake and signaling functions; however, the mechanisms enabling this transition remain poorly understood. How residual roots survive canopy removal, initiate new growth, and coordinate hormonally with emerging shoots, particularly through cytokinin and auxin signaling (Rogers and Benfey, 2015; Sakakibara, 2021; Yuan et al., 2024), is central to explaining early ratoon vigor and stability. Moreover, root function determines the competitive balance among tillers by differentially supporting nodal positions. A failure in timely root functional turnover can therefore translate directly into intensified competition and selective abortion of weaker tillers.

Beyond immediate physiological responses, the role of biological memory remains largely unexplored. Evidence that stresses experienced during the main crop affect subsequent ratoon performance suggests the persistence of a stress legacy across harvest events (Huang et al., 2022). Such legacy effects may precondition not only regenerative capacity, but also the competitive landscape among buds by altering hormonal sensitivity, reserve allocation, or growth priorities, potentially mediated by plant–microbe interactions. Whether such memory is mediated through chromatin modification, DNA methylation, plant–microbe interactions interacting with host epigenetic mechanisms, or other epigenetic mechanisms and how it is maintained and recalled in axillary buds represent important frontiers with implications for priming regenerative resilience (Charng et al., 2023; Liu et al., 2022; Sato and Yamane, 2024).

Finally, these mechanistic insights point toward the need for a more deliberate breeding strategy (Henry, 2024; Yang et al., 2025). Quantifiable and potentially heritable traits underpinning ratooning, including bud competence, delayed root senescence, and efficient reserve mobilization, have the ability to regulate internal competition among tillers, yet they have rarely been targeted explicitly. This raises a fundamental challenge for future crop improvement. Can regenerative capacity be designed rather than accommodated? Addressing this question and clarifying potential trade-offs with main crop yield will be essential for integrating ratooning into next-generation cereal breeding programs.

5. Conclusions

In summary, this review reframes ratooning not as a sequence of isolated post-harvest responses, but as a biologically continuous, whole-plant regenerative process that unfolds across seasons. Rather than being governed by any single factor, ratoon performance emerges from the coordinated interaction of bud competence, stubble-mediated transport and storage, root–shoot re-synchronization, and spatially structured yield formation. While each of these components has been described to varying degrees, they are still predominantly investigated in isolation. As a consequence, ratoon outcomes are often interpreted through empirical correlations or management effects rather than through integrated biological mechanisms. This fragmentation limits both predictive understanding and rational intervention. Addressing this disconnect by treating regeneration as a system-level process is therefore essential for moving beyond incremental management optimization toward a mechanistic and design-oriented understanding of ratoon system stability and productivity.

Abbreviations

Not applicable.

Availability of data and materials

Not applicable.

Authors' contributions

Dongliang Xiong: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Conceptualization. Yang Xiao: Writing – review & editing, Investigation. Jing Zhao: Writing – review & editing, Investigation, Data curation. Gen Li: Writing – review & editing, Investigation, Data curation. Jianliang Huang: Writing – review & editing, Project administration.

Declarations of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Given his role as Editor-in-Chief, Dongliang Xiong had no involvement in the peer review of this article and has no access to information regarding its peer review, Full responsibility for the editorial process for this article was delegated to Shaobing Peng.

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Dongliang Xiong*, Yang Xiao, Jing Zhao, Gen Li, Jianliang Huang
National Key Laboratory of Crop Genetic Improvement, Hubei Hongshan Laboratory, MARA Key Laboratory of Crop Ecophysiology and Farming System in the Middle Reaches of the Yangtze River, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei 430070, China

* Corresponding author.
E-mail address: dlxiong@mail.hzau.edu.cn (D. Xiong).