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The Race to Flourish: Evaluating Natural Variation of Early Growth Rates in Rice

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ABSTRACT

Direct-seeded rice is a promising practice for sustainable rice productivity due to its ability to enhance ecosystem services. The use of rice varieties with shorter growth periods has become crucial for effective crop rotation. However, shorter growth periods often result in lower grain yields. Enhancing early growth in these short-duration rice varieties could help offset yield losses, but the genetic potential for early growth remains largely untapped. In this study, we investigated early growth in 90 rice genotypes under field conditions. Significant variation in plant growth was observed at 15, 25, and 35 days after sowing (DAS), with differences becoming more pronounced over time. Seed size had no significant effect on variation in growth rate. Hierarchical clustering analysis grouped the genotypes into five distinct growth patterns: Consistently Slow, Early Surge, Steady Moderate, Delayed Vigor, and Consistently Rapid. These patterns exhibited distinct trends in absolute growth rate (AGR) and relative growth rate (RGR). The Consistently Rapid and Early Surge groups showed higher early growth, whereas Delayed Vigor displayed accelerated growth at later stages. Contrary to traditional assumptions, the RGR during the early growth stage was not constant but varied significantly over time. RGR was primarily correlated with net assimilation rate (NAR) rather than leaf mass ratio (LMR) or specific leaf area (SLA). Size-standardized RGR and its components followed similar trends, indicating consistent growth dynamics across genotypes. These findings highlight distinct early growth patterns among rice genotypes, providing valuable insights for breeding programs aimed at improving early vigor and optimizing yield in short-duration rice varieties.

1 | Introduction

By 2050, global food production is expected to encounter significant challenges, as it will need to double to meet the demands of an estimated 9.8 billion people (Giller et al. 2021). Factors such as population growth, urbanization, and rising affluence are expected to drive a surge in demand, particularly for protein-rich foods like meat and dairy products (Colgrave et al. 2021; Habib et al. 2025). To meet this increasing food demand despite limited arable land and stagnant yield growth, it is crucial not only to expand cultivated areas but also to enhance the multiple cropping index (Wu et al. 2018; Zhang et al. 2021). In this context, crop rotation is vital for sustaining crop production in China, particularly in the southern regions where rice fields are concentrated (Xie et al. 2023). The rotation system helps maintain soil fertility, manage pests and diseases, and optimize resource use, all of which are essential for stable and higher yields (Yang, Xiong, et al. 2024; Chang et al. 2025; Nauanova et al. 2025). However, the strict seasonality of crop growth within rotation systems imposes rigorous requirements on the growth duration of crops. Traditionally, seedling transplanting has been used to shorten the field growth period, allowing for efficient crop rotation. Yet, this method is becoming less viable due to declining rural labor availability and rising costs (Peng 2014). Direct seeding has been proposed as an alternative, requiring less labor but eliminating the nursery period, thus necessitating the use of crop varieties with shorter growing periods to maintain the effectiveness of the rice field rotation system (Liu et al. 2015; Xu et al. 2019).

Historically, it was assumed that short-duration rice varieties produced lower yields than longer-duration ones due to reduced solar radiation exposure, which impacted biomass accumulation and yield (Vergara et al. 1966). However, recent studies have shown that the rapid early growth rate of short-duration varieties may offset the yield losses associated with their shorter growth periods (Wei et al. 2022; Pan et al. 2023; Yang, Xiang, et al. 2024). This suggests that enhancing early growth could be a critical strategy for increasing grain yield in rice-based crop rotation systems. Rapid early crop growth, which reflects a crop's ability to develop quickly before canopy closure, is also considered vital for resource use efficiency, as it enables quick canopy establishment and the efficient acquisition of essential resources like light, water, and nutrients (Rebolledo et al. 2012; Xiong 2024).

To quantitatively assess early growth, researchers frequently utilize the absolute growth rate (AGR) and relative growth rate (RGR) as key indicators of biomass accumulation (Evans 1972; Hilty et al. 2021). AGR quantifies the increase in biomass over a defined period, whereas RGR provides a relative measure by accounting for the growth rate with respect to the initial biomass (see Paine et al. 2012 and references therein). RGR is particularly valuable because it normalizes growth based on the organism's initial size, providing a more consistent metric than AGR (Blackman 1919; Paine et al. 2012; Lamont et al. 2023). In rice, substantial intraspecific variation in RGR presents an unexploited opportunity for crop improvement (Rebolledo et al. 2015; Subramanian et al. 2025). However, in most studies, RGR is typically estimated by harvesting plants at two distinct time points, calculating the difference between the natural logarithms of their biomass, and dividing by elapsed time (Rebolledo et al. 2012, 2015; Fletcher et al. 2022; Gómez-Fernández and Milla 2022). This approach assumes exponential biomass accumulation over time, which presumes that all newly acquired dry matter directly contributes to photosynthetic carbon uptake (Paine et al. 2012; Hilty et al. 2021). However, this assumption is flawed in higher plants, even in the early growth stages, due to factors such as the accumulation of non-photosynthetic biomass in roots, leaf self-shading, and variability within and between leaves (Paine et al. 2012; Tessmer et al. 2013; Pommerening and Muszta 2016; Hilty et al. 2021). As a result, respiration costs rise as total plant biomass increases, while carbon acquisition is confined to the photosynthetic biomass, leading to a decline in biomass accumulation relative to total biomass as the plant matures. Consequently, traditional growth rate calculations fall short in capturing the complexities of growth dynamics over time and in elucidating the physiological mechanisms that drive rapid early growth. The power-law model provides a more accurate alternative to the exponential model for describing how RGR changes over time and with increasing biomass (Paine et al. 2012). In this model, a β value of 0 signifies a linear relationship between biomass and growth. A β between 0 and 1 indicates a progressively decreasing in RGR as biomass increases. A β of 1 corresponds to an exponential model, where the RGR remains constant regardless of biomass. When β exceeds 1, the RGR increases with increasing biomass.

Trait-based mechanisms, particularly those related to biomass allocation and plant economics, have been proposed to influence the relationship with RGR (Poorter et al. 2012 and references therein). Theoretically, RGR can be divided into three key components (Hunt and Cornelissen 1997; Shipley and Meziane 2002): net assimilation rate (NAR), leaf mass ratio (LMR), and specific leaf area (SLA). Some studies suggest that variations in RGR are largely driven by differences in LMR, and especially by SLA, with plants exhibiting higher SLA generally having higher RGR (James and Drenovsky 2007; Osone et al. 2008; Fletcher et al. 2022). Conversely, other research indicates that variations in RGR may be influenced by NAR, particularly among closely related taxa (Atkin et al. 2006; Li et al. 2016). The significance of these components in determining RGR can also vary depending on plant size. It is important to acknowledge that these components are interdependent, which can lead to mathematical confounding when comparing them. Therefore, careful interpretation and the identification of functional traits associated with RGR and its components may be necessary when studying the factors influencing RGR variation.

The aim of the current study was to evaluate the growth performance of 90 rice accessions under field conditions in 2021, and, in 2022, a sub-group containing 12 genotypes was grown under the same conditions to (1) explore the intraspecies variations in biomass accumulation patterns and the dynamics of AGR and RGR during the early growth stages; (2) uncover how the components of RGR contribute to early rapid growth; and (3) analyze the relationships between growth and morphological traits.

2 | Materials and Methods

2.1 | Plant Materials and Growth Conditions

A two-year field trial was conducted starting on June 4, 2021, and on May 22, 2022, during the early growth stage. In the first year, 90 rice genotypes were evaluated, and 12 of these were selected for further study in 2022 based on their different types of early growth rates observed in 2021. Details of the experimental materials used in both years are presented in Table S1.

The 2021 field experiment was conducted in Wuxue County, Huanggang, Hubei, China (30°01′ N, 115°78′ E), using a randomized complete block design. Each genotype was assigned to four replicates, resulting in 360 plots used to screen early seedling vigor across the 90 genotypes. Twenty-four grams of pre-germinated rice seeds were broadcast-sown into wet, puddled plots, each covering an area of 4 m^2. Before sowing, nitrogen (72 kg N ha^{-1}, urea), phosphorus (90 kg P ha^{-1}, single superphosphate), and potassium (90 kg K ha^{-1}, potassium chloride) were manually broadcast as base fertilizers in all the plots, and the paddy field was carefully leveled. During the experimental period, water levels were well maintained, and weeds, diseases, and pests were effectively controlled with chemical pesticides. The 2022 field experiment was conducted in Wuhan at the Crop Physiology and Production Center, Hubei Province, China (30°46′ N, 114°36′ E). Seeds of the 12 selected genotypes were sown in four replicates, totaling 48 plots. All management practices were kept the same as those in 2021.

The precipitation and temperature for the 2 years are shown in Figure S1. In 2021, rainfall was significantly higher than in 2022. During the growing season in 2021, total precipitation reached 312.1 mm, while in 2022, it was less than half that amount, at just 115.0 mm. The average temperature during the experimental seasons in both years ranged from 22°C to 32°C.

2.2 | Sampling and Growth Traits Measurements

Five individual plants from each plot were sampled at 15, 25, and 35 days after sowing (DAS) in 2021. In 2022, growth traits were measured at 4, 10, 15, 19, 24, 28, and 36 DAS to increase the sampling frequency and thereby more precisely simulate plant growth during the early stage. Plants with part of the root system were sampled and watered before measurements were conducted. Measurements included plant height (PH, cm), number of tillers (TN), leaf area (LA, cm^2), leaf dry weight (LDW, g), stem dry weight (StemDW, g), and shoot dry weight (SDW, g). Plant height was recorded from the stem base to the top of the plant after the longest leaf had fully extended. The dry weight of the above-ground portion was determined after oven drying at 80°C for 72 h. Leaf area was measured using ImageJ software (Wayne Rasband/NIH, Bethesda, MD, USA). Specific leaf area (SLA, $cm^2\ g^{-1}$) and leaf mass ratio (LMR, $g\ g^{-1}$) were calculated as the ratio of leaf area to leaf dry weight and the ratio of leaf dry weight to shoot dry weight, respectively. As the root system was severely damaged during the sampling and watering, we did not measure root traits in this study. Phenotypic variance (PV) and phenotypic coefficient of variance (PCV) were calculated according to the methods mentioned in Acevedo-Siaca et al. (2021). In short, PV quantifies variability by representing the average squared deviation from the mean, and PCV is calculated by dividing the standard deviation of a trait by its mean.

2.3 | Growth Analysis

In this study, biomass accumulation was assessed through both absolute growth rate (AGR) and relative growth rate (RGR), calculated using two distinct methods. Initially, average growth rates were derived from biomass measurements between two sampling points. The average AGR between two points was calculated as $(M_2 - M_1)/(t_2 - t_1)$, while the average RGR was determined as $(\ln(M_2) - \ln(M_1))/(t_2 - t_1)$. Here, M_1 and M_2 represent biomass $M = \left(M_0^{1-\beta} + rt(1-\beta)\right)^{\frac{1}{1-\beta}}$ amounts at times t_1 and t_2, respectively (with $t_2 > t_1$).

The second method involved estimating real-time AGR and RGR by fitting a biomass growth curve to a power model (Paine et al. 2012):where M is the biomass at time t, M_0 is the initial biomass, r denotes the intrinsic growth rate that influences overall growth speed, and β is a parameter defining the growth curve shape. For different β values, the model adapts: a β near 1 yields exponential growth, $1 > \beta > 0$ shows decelerating growth, and $\beta > 1$ suggests an accelerating growth pattern. According to this model, AGR over time is:

$$\mathrm{AGR} = r\left(M_0^{1-\beta} + rt(1-\beta)\right)^{\frac{1}{1-\beta}}$$

and RGR over time is given by:

$$\mathrm{RGR} = \frac{r}{M_0^{1-\beta} + rt(1-\beta)}$$

Since RGR is influenced by plant size, comparing genotypes of varying sizes has been subject to criticism (Turnbull et al. 2008, 2012; Lamont et al. 2023). To address this, size-standardized RGR (sRGR) was calculated by fitting a growth curve to plants sampled from each plot, and then extracting RGR values at two common reference sizes, 2.5 and 5.0 g (Gómez-Fernández and Milla 2022).

In the current study, components of relative growth rate (RGR) and size-standardized relative growth rate (sRGR) were calculated. For the RGR components, RGR values for plants sampled from each plot at 15, 25, and 35 DAS were extracted from the fitted growth curve, and measured specific leaf area (SLA) and leaf mass ratio (LMR) were used to calculate the net assimilation rate (NAR) following Hunt (1982) equation: RGR = SLA × LMR × NAR.

To calculate the components of sRGR, individual growth curves for leaf dry mass and leaf area over time were modeled using a power function. Leaf area and mass were then estimated at the point when each plant in the plot reached a defined reference size. These estimates allowed us to determine size-standardized LMR (sLMR), representing the ratio of leaf mass to total plant mass at the reference size, and size-standardized SLA (sSLA), representing the ratio of leaf area to leaf mass at the reference size (Gómez-Fernández and Milla 2022).

2.4 | Statistical Analysis

Differences between genotypes were assessed through one-way ANOVA with Tukey's test for pairwise comparisons at a significance level of 0.05, using the "*multcomp*" package in R. The "*nlme*" package in R was used to fit the power growth model and simulate real-time AGR and RGR. The relative importance of plant tissues in determining biomass was estimated using the Random Forest method with the "*randomForest*" package, and the hierarchical clustering analysis was adopted to cluster the genotypes with different growth patterns. Data analysis and visualization were performed using the "*tidyverse*" "*dplyr*" "*cowplot*" and "*readxl*" packages. All analyses and visualizations were completed using R version 4.4.1 (R Core Team 2024).

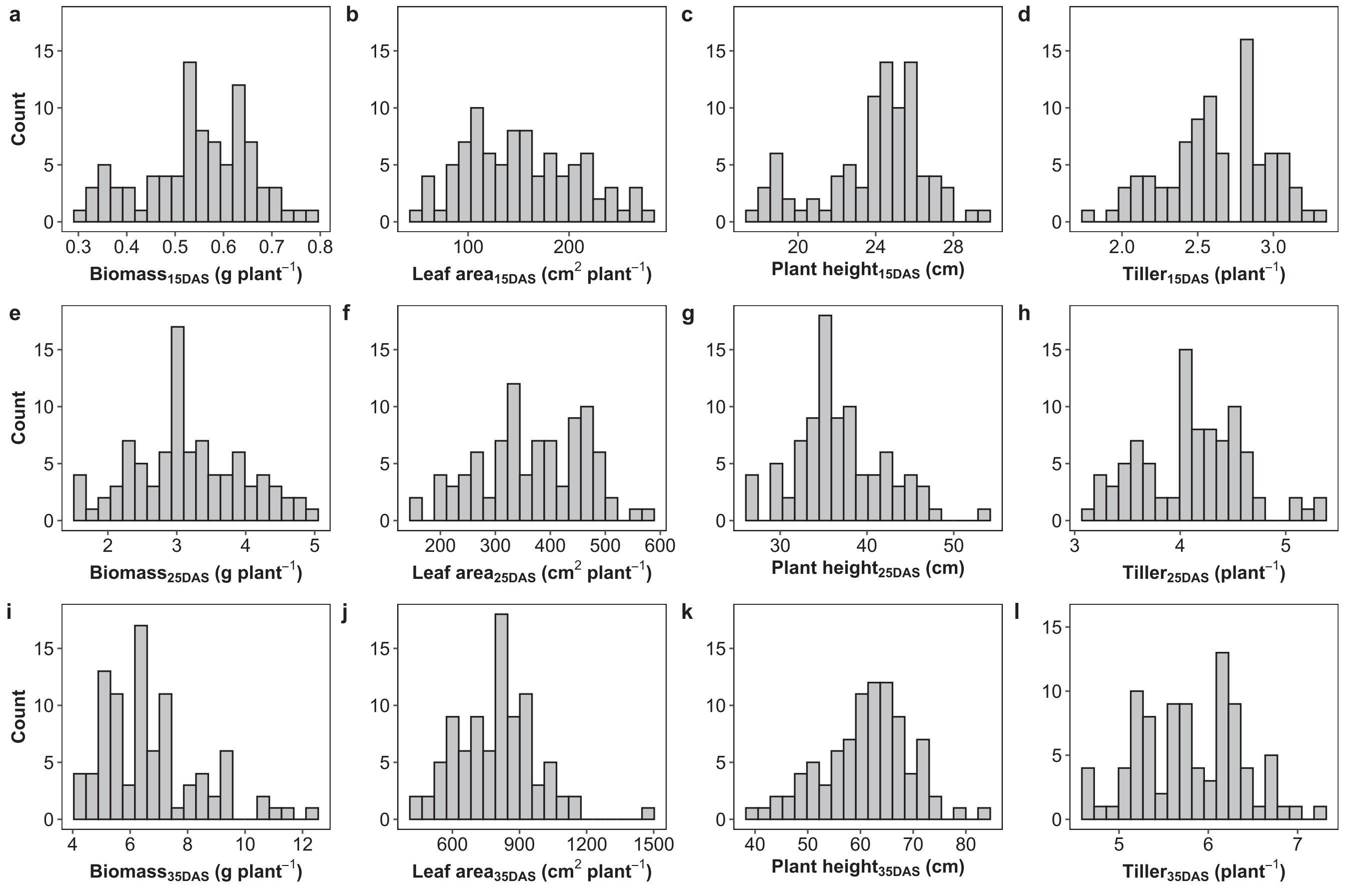

FIGURE 1 | Frequency distribution of phenotypic values for 90 rice accessions at three different sampling times: (a–d) 15 days after sowing (DAS), (e–h) 25 DAS, and (i–l) 35 DAS. Panels (a), (e), and (i) show biomass; (b), (f), and (j) show leaf area; (c), (g), and (k) show plant height; and (d), (h), and (l) show tiller numbers.

3 | Results

The distributions of growth trait values for the 90 genotypes at 15, 25, and 35 days after sowing are shown in Figure 1. Significant variations in aboveground biomass were observed among genotypes at each stage, with differences becoming more pronounced as the plants grew. At 15 DAS, the mean biomass for each genotype ranged from 0.31 to 0.79 g plant^{-1}, while at 35 DAS, it ranged from 4.19 to 12.27 g plant^{-1} (Table S2). The increase in intraspecies variation is further supported by a rise in phenotypic variance (PV), which represents the total variation in observable traits within a population. PV increased from 0.01 to 0.63 and then to 3.03 at 15, 25, and 35 DAS, respectively. Other growth traits, including leaf area per plant, plant height, and tiller number, followed a similar pattern to biomass. Among those traits, leaf area per plant exhibited the highest phenotypic variance, while tiller number showed the lowest variance for all the sampling dates (Figure 1; Table S2). For the 12 genotypes in 2022, similar distribution patterns of growth traits were observed over time and across different traits (Table S2). Aboveground biomass ranged from 0.002 to 0.004 g plant^{-1} at 4 DAS and from 2.15 to 5.50 g plant^{-1} at 36 DAS. Leaf area displayed greater variation among genotypes, ranging from 0.22 to 0.82 cm^2 plant^{-1} at 4 DAS and from 243 to 848 cm^2 plant^{-1} at 36 DAS. Interestingly, having a large biomass early on does not guarantee continued growth dominance. As shown in Figure S2, a genotype with lower biomass at 15 DAS may surpass a larger biomass genotype by 25 or 35 DAS. Similarly, a genotype with an early biomass advantage may lose this advantage in a later growth period.

Based on the pattern of biomass increment from 15 to 25 and 25 to 35 days after sowing, the examined genotypes were categorized into five distinct groups using hierarchical clustering analysis (Figure 2). Genotypes that exhibited a relatively slow increase in biomass during both sampling intervals were classified as “Consistently Slow” (CS). Those that demonstrated rapid growth between 15 and 25 DAS, followed by a decline in growth rate between 25 and 35 DAS, were grouped into the “Early Surge” (ES) category. Genotypes with a steady, moderate increase in biomass were categorized as “Steady Moderate” (SM). The “Delayed Vigor” (DV) group included genotypes that showed a more rapid biomass increase between 25 and 35 DAS than between 15 and 25 DAS. Finally, genotypes that consistently exhibited rapid biomass growth throughout both intervals were classified under “Consistently Rapid” (CR). It is worth noting that the number of genotypes in each category varies greatly, with CS, SM, and DV having the largest number of genotypes, while CR has the fewest.

Further analysis of the relative importance of leaf area, plant height, and tiller number in determining plant biomass within these growth patterns revealed distinct differences across the

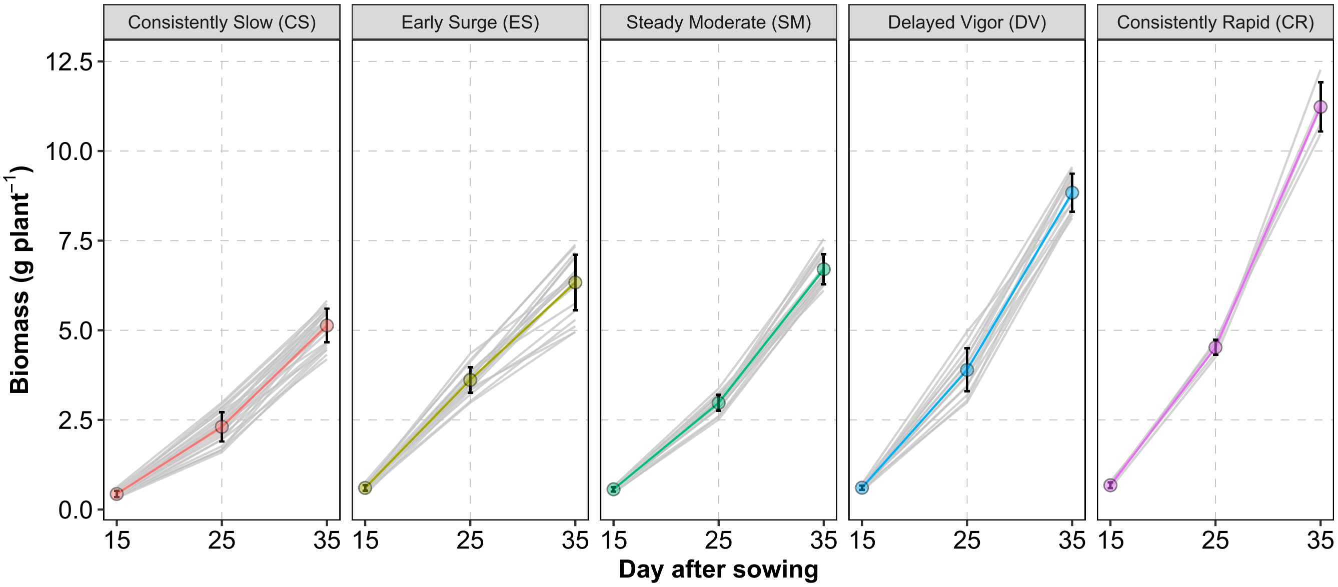

FIGURE 2 | Five growth patterns, identified through hierarchical clustering analysis of 90 rice accessions, correspond to biomass measurements taken at three distinct growth stages. The gray lines indicate the values for each genotype, while the dots and bars represent the mean values and standard errors for these genotypes on the specified sampling days.

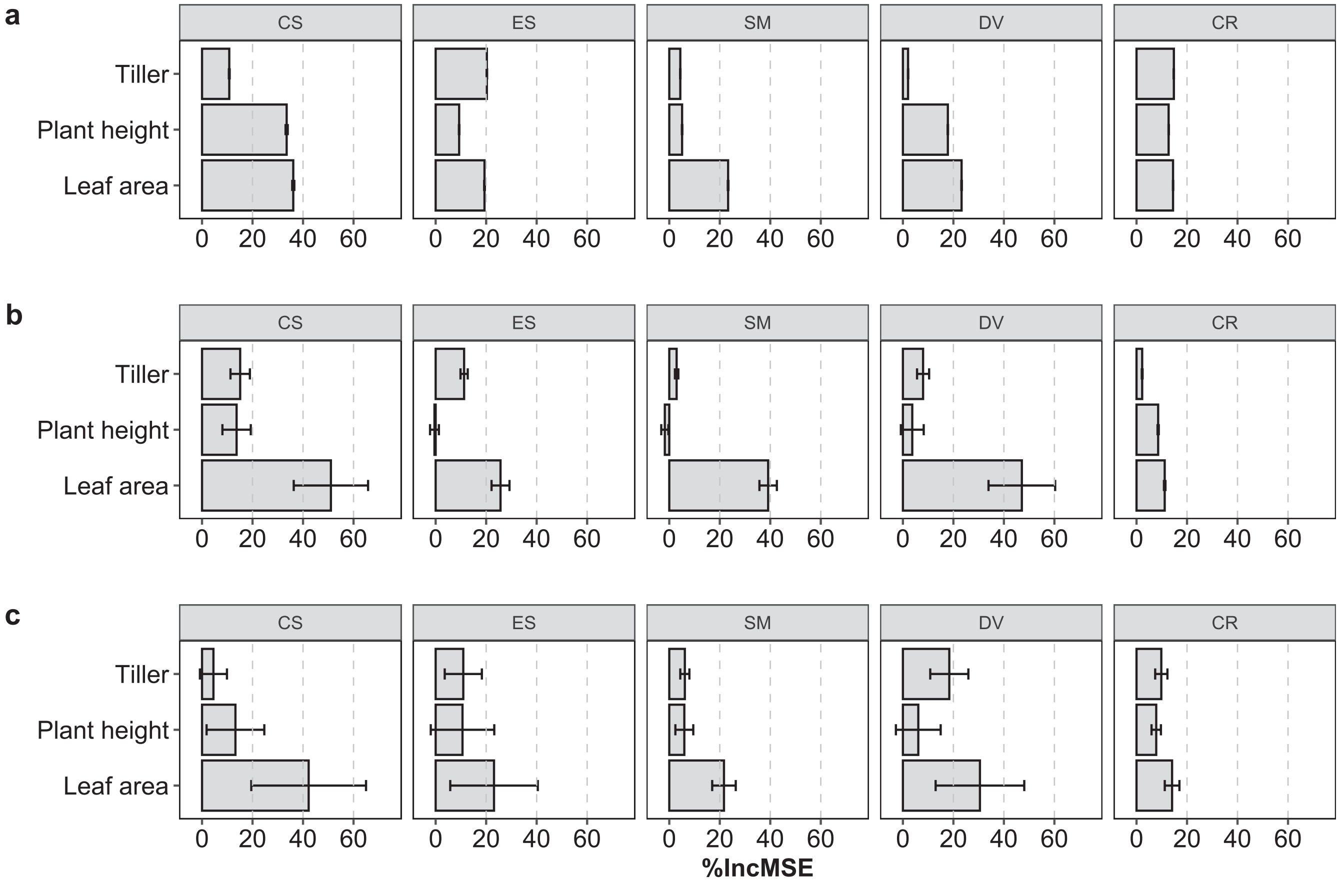

FIGURE 3 | The relative importance of leaf area, plant height, and tiller numbers in determining plant biomass. The percentage increase in mean squared error (%IncMSE) was estimated by permuting these variables in a random forest model. This assessment applies to each clustered growth pattern: CS (Consistently Slow), ES (Early Surge), SM (Steady Moderate), DV (Delayed Vigor), and CR (Consistently Rapid) at the 15 (a), 25 (b) and 35 (c) days after sowing. Error bars represent the standard deviation of the increase in MSE.

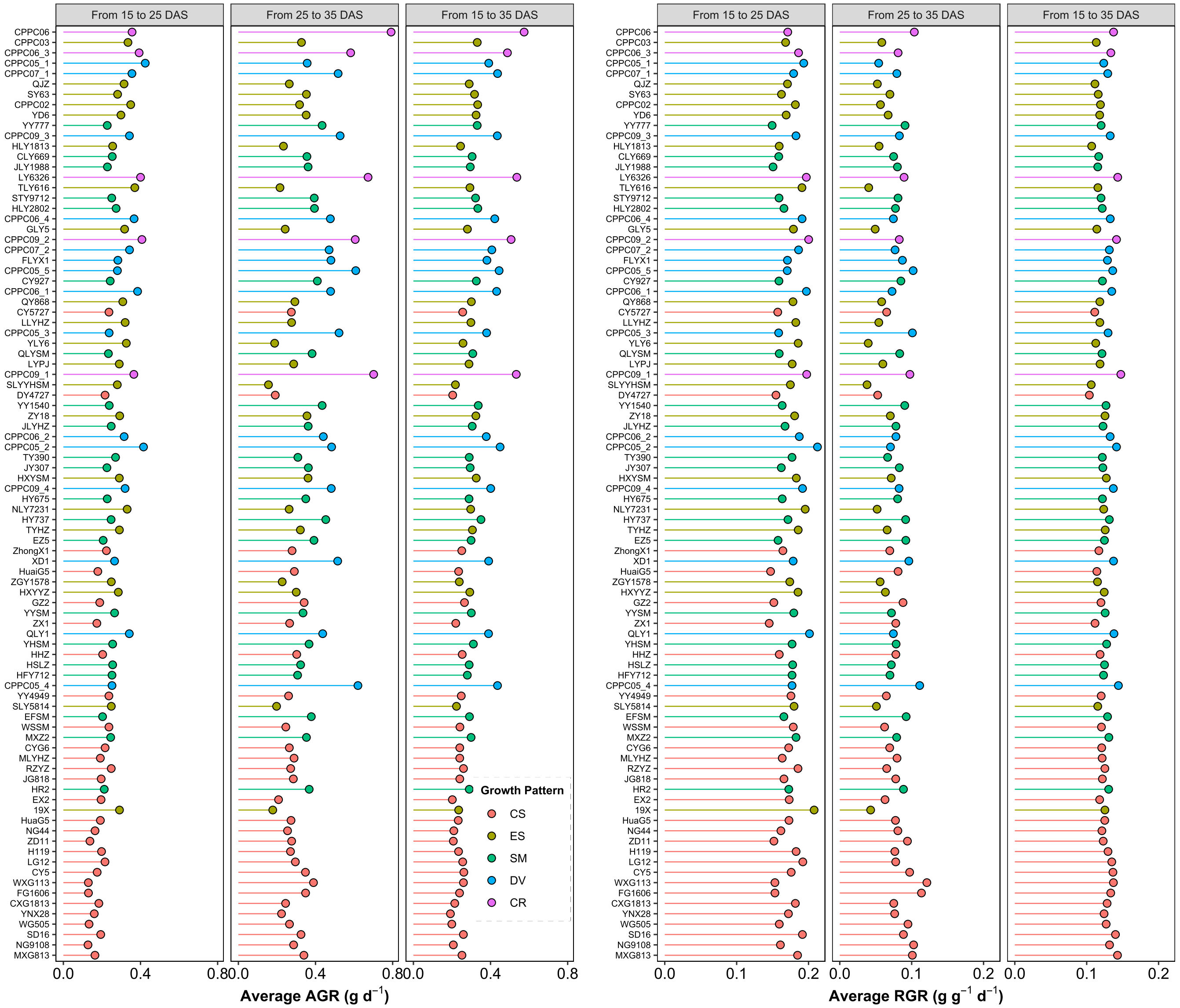

FIGURE 4 | The genotype-averaged absolute growth rate (AGR) and relative growth rate (RGR) for 90 rice accessions over different growth periods. Different colors represent clustered growth patterns: CS (Consistently Slow), ES (Early Surge), SM (Steady Moderate), DV (Delayed Vigor), and CR (Consistently Rapid). The accessions are ordered by ascending mean biomass observed 15 days after sowing, as shown in Figure S2.

clusters (Figure 3). The percentage increase in mean squared error (%IncMSE) was assessed using a random forest model. The analysis showed that, overall, leaf area was the most critical determinant of biomass, followed by tiller number and plant height. However, CR genotypes showed a relatively balanced importance among all three traits. The standard deviation of the increase in MSE was consistent across the traits, indicating the robustness of these findings.

The average absolute growth rate (AGR) and relative growth rate (RGR), calculated using traditional plant growth analysis, showed significant variation among the estimated accessions and across different growth periods (Figure 4). To better understand the dynamics of these growth rates over time, the accumulated biomass of each genotype was modeled using a power equation (Figures S3 and S4). As shown in Figure S4 for the 12 genotypes in 2022, the modeled biomass closely aligned with the measured biomass, with the fitted line (slope of 1.02 and intercept of −0.01) being nearly identical to the 1:1 line. Using the genotype-specific power model equations, we calculated the instantaneous AGR and RGR, which are illustrated in Figure S5. The results clearly indicate that while AGR increases over time for most growth patterns, RGR significantly declines as development progresses. Notably, these trends were consistent across the different biomass accumulation pattern groups. The five rice growth pattern groups were distinctly separated by the dynamic growth rate analysis: CS and SM exhibited gradual and balanced growth, characterized by slow increases in AGR and steady declines in RGR over time. In contrast, ES and CR showed more vigorous early growth, with ES stabilizing after an initial surge and CR maintaining high growth rates throughout. DV began with relatively slow growth but accelerated later, showing a delayed yet rapid increase in both AGR and RGR.

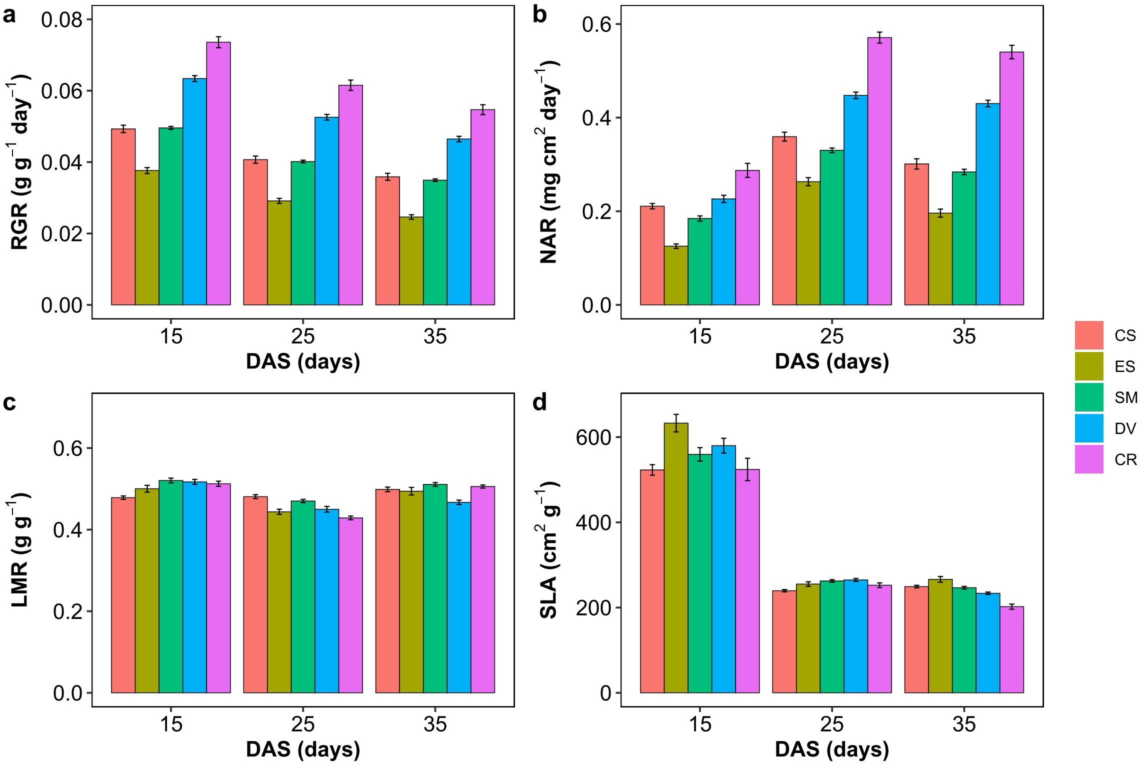

FIGURE 5 | Variation in (a) relative growth rate (RGR), (b) net assimilation rate (NAR), (c) leaf mass ratio (LMR), and (d) specific leaf area (SLA) among the five clustered growth patterns at three sampling days after sowing (DAS). Different letters indicate significant differences among growth patterns at identical DAS, as determined by Tukey's post hoc test at a significance level of $p < 0.05$. Growth patterns are labeled as CS (Consistently Slow), ES (Early Surge), SM (Steady Moderate), DV (Delayed Vigor), and CR (Consistently Rapid).

The variation of RGR and its associated components, including net assimilation rate (NAR), leaf mass ratio (LMR), and specific leaf area (SLA), among the five clustered growth patterns across three sampling DAS is shown in Figure 5. The differences in RGR between growth pattern groups were consistent with the differences in NAR at each of the three sampling dates. The variation in LMR between growth pattern groups showed some variability, though the differences were less pronounced compared to RGR and NAR. In contrast, SLA exhibited distinct differences between growth pattern groups, particularly at the early sampling date, with patterns that had higher SLA at 15 DAS generally showing a decrease as the plants grew. Across genotypes, RGR was strongly correlated with NAR at all three sampling DAS but showed no correlation with LMR or SLA on any sampling day, except for SLA at 35 DAS (Figure S6).

Since RGR typically depends on plant size, we analyzed RGR and its components at two different plant size levels (Figure 6). The size-standardized RGR (sRGR) decreased as plant size increased. Additionally, the differences in sRGR components between growth groups were similar to those of RGR components measured at the sampling DAS. Across genotypes, sRGR was significantly correlated with sNAR at both plant sizes (Figure S7). Although sRGR was significantly correlated with sLMR at a plant size of 5.0 g and with sSLA at a plant size of 2.5 g, the R^2 values for these correlations were very small. In this study, we also analyzed the effects of seed size on growth rate. As shown in Figure 7, grain weight did not differ significantly between the growth pattern groups. Furthermore, no correlations were observed between grain weight and either RGR or sRGR.

4 | Discussion

4.1 | Non-Constant RGR Patterns During the Early Growth Stage

Growth analysis is often used to describe the development of individual plants, typically under the assumption that biomass growth follows an exponential pattern (Evans 1972). This assumption suggests that the relative growth rate (RGR) remains constant throughout the growth period. In practice, RGR is frequently estimated by harvesting plants at two specific time points, calculating it based on the difference in the natural logarithms of biomass values, and then dividing this difference by the time elapsed between the harvests (Rebolledo et al. 2012; Fletcher et al. 2022). In this study, plant samples were harvested multiple times (3 and 7 times in 2021 and 2022, respectively) within the first 35 DAS. The results showed that the RGR calculated based on two harvest points varied across different sampling intervals. Our results demonstrated that the calculated RGR is influenced by the chosen sampling intervals and the initial condition of the plants, as proposed in other studies. Indeed, the assumption of exponential growth presumes that all newly accumulated dry matter contributes to photosynthetic carbon uptake. However, this is inaccurate

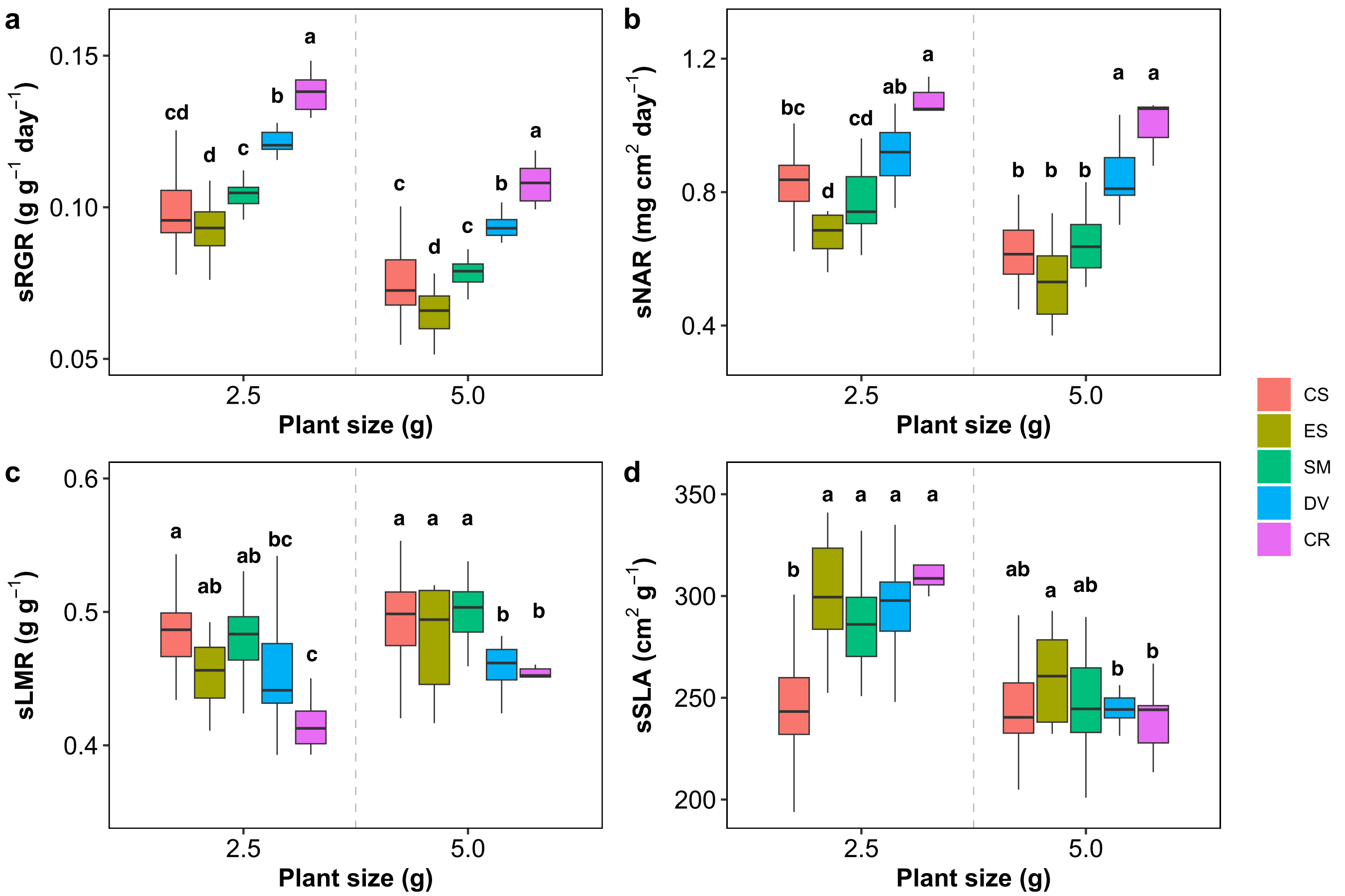

FIGURE 6 | Size-standardised (a) relative growth rate (sRGR), (b) net assimilation rate (sNAR), (c) leaf mass ratio (sLMR), and (d) specific leaf area (sSLA) among the five clustered growth patterns. Boxplots illustrate the median, 25th, and 75th percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Distinct letters denote significant differences among growth patterns at the same plant size, as identified by Tukey's post hoc test at a significance level of 0.05. Growth patterns are labeled as CS (Consistently Slow), ES (Early Surge), SM (Steady Moderate), DV (Delayed Vigor), and CR (Consistently Rapid).

for higher plants due to factors such as the buildup of non-photosynthetic biomass in roots, leaf self-shading, and variations within and between leaves (Shipley and Meziane 2002; Poorter et al. 2012).

To better capture variations in growth over time, the real-time growth rates can be estimated by fitting growth models (Hunt 1982; Paine et al. 2012). These growth models fall into two categories: those assuming a final asymptotic size and those that do not (Paine et al. 2012 and references therein). While the concept of an asymptotic size is common in population studies, it is more complex when applied to individual plants. Plant growth may plateau due to resource limitations or developmental stages, such as flowering. The choice between asymptotic and non-asymptotic models depends on the variable being measured and the study duration. Asymptotic models are appropriate for studies spanning a plant's full life cycle, while non-asymptotic models, which allow for continuous growth, are useful for early stages, such as seedling growth. In the current study, the growth of early rice biomass was fitted using a power model, which is a non-asymptotic type. The fittings of the power model also revealed that the growth rates of rice seedlings are highly variable over the growth period and among genotypes.

4.2 | The Early Growth Rate of Rice Is Independent of Seed Mass

By 15 days after sowing, biomass differences had more than doubled, and by 35 DAS, variation among genotypes had increased to over threefold. To analyze these early growth patterns further, we categorized the 90 rice genotypes into five groups based on their biomass accumulation dynamics. Some genotypes displayed rapid early growth that later slowed, while others exhibited slow initial growth that accelerated later (Figure 2). Still, other genotypes maintained consistently slow, moderate, or fast growth throughout the observation period. Seed traits, particularly seed mass, are considered crucial factors for regulating initial plant growth (Turnbull et al. 2008, 2012; Simpson et al. 2021; Lamont et al. 2023). Larger seeds generally offer an early growth advantage due to their greater resource reserves, which enhance seedling establishment, early vigor, and competitiveness in resource-limited environments. However, in our study, no differences in seed size, as represented by grain weight, were observed among the groups (Figure 7). Moreover, no significant correlations were found between grain weight and RGR, whether assessed on a time basis or on a mass basis. Recent studies have indicated that the relationship between seed size and growth rate is complex and not necessarily straightforward

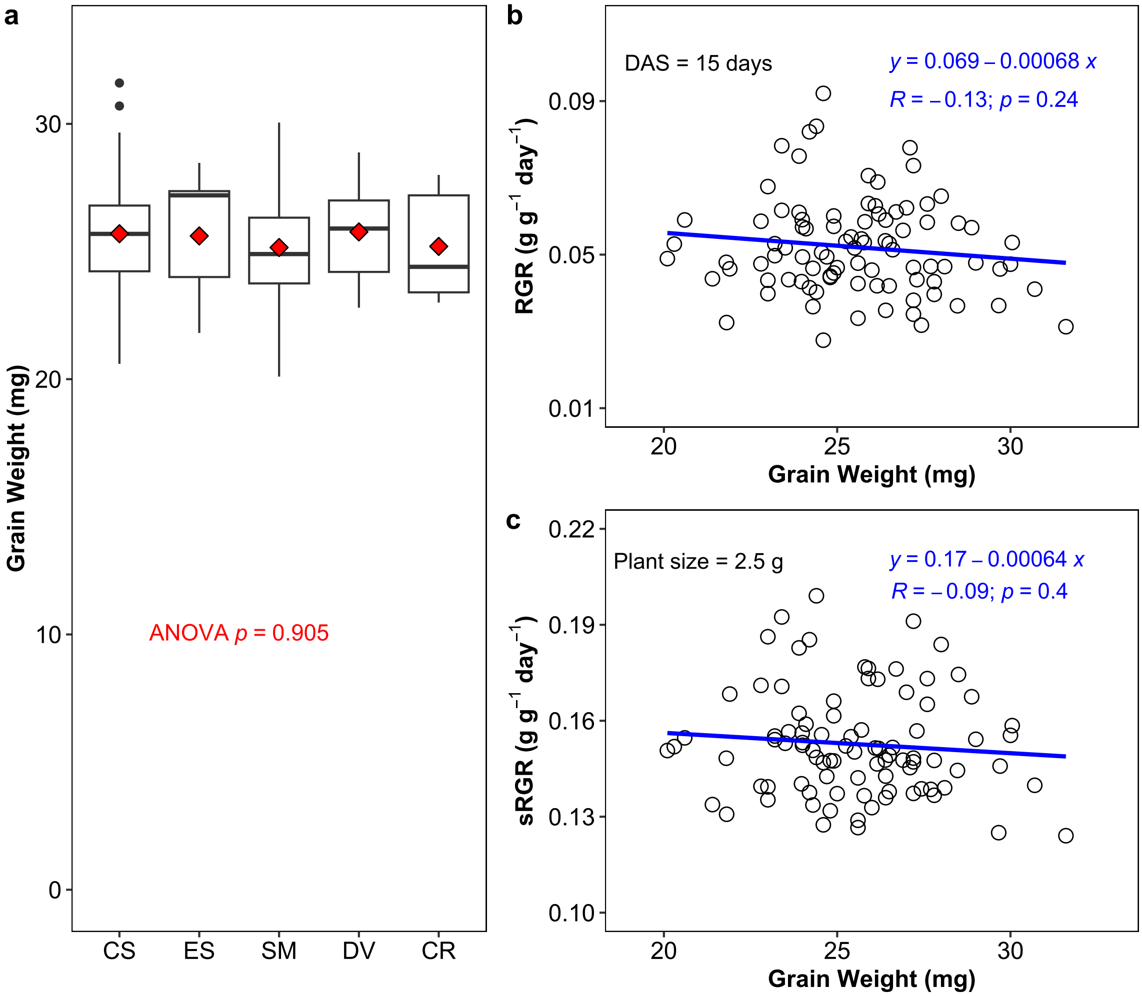

FIGURE 7 | Grain weight for five growth patterns and its relationships with relative growth rate (RGR) at 15 days after sowing (DAS) and size-standardized relative growth rate (sRGR) at a biomass of 2.5 g. Boxplots in panel (a) display the median, 25th, and 75th percentiles of grain weight for each group, with whiskers extending to 1.5 times the interquartile range. The red squares represent the mean values. Differences among growth patterns were assessed by one-way ANOVA with Tukey's post hoc test at a significance level of 0.05. Panels (b) and (c) show correlations estimated by linear model fitting. Growth patterns are categorized as CS (Consistently Slow), ES (Early Surge), SM (Steady Moderate), DV (Delayed Vigor), and CR (Consistently Rapid).

(Hanley et al. 2004; Winkler et al. 2024). The growth advantage observed in certain genotypes may therefore be attributed to the quality and physiological traits of the seeds, such as high conversion efficiency of seed reserves and more efficient nutrient mobilization, rather than simply to seed size or weight. Indeed, Huang et al. (2017) further emphasized that while seed size may not directly determine growth, the composition and functionality of the seeds—such as amylase activity and reserve mobilization—play a crucial role in determining seedling vigor and growth rate. Further studies are needed to elucidate how specific seed traits regulate the initial growth of plants.

4.3 | Relative Importance of RGR Components in Driving Early Rapid Growth

As mentioned earlier, RGR can be divided into four components, and the relative importance of these components in determining plant growth varies across studies and is strongly influenced by environmental conditions (Poorter 1999). In low-light environments, SLA and LMR tend to play a more significant role in influencing differences in RGR between species. However, under high-light conditions, the importance of NAR increases. Since the rice plants in our study were cultivated in an open field, we observed that the variation in RGR among clustered groups was primarily driven by NAR, though LMR and SLA also contributed to some extent.

Growth variations among groups likely relate to the transition from heterotrophic to autotrophic growth, a critical phase in early plant development (Hanley et al. 2004). During the heterotrophic phase, seedlings depend on stored energy reserves, such as seed carbohydrates, for growth. As these reserves are depleted, the plant transitions to autotrophic growth, relying on photosynthesis for energy production and biomass accumulation. Genotypes with rapid early growth likely transitioned to autotrophic growth more efficiently or rapidly. This enabled them to maximize the production of photosynthetic energy at an earlier stage. In contrast, genotypes with slower early growth may have experienced a delayed or less efficient transition, relying on seed reserves for a longer period. As plants transition to autotrophic growth, their ability to capture light and convert it into biomass becomes essential. Some plants accelerate growth after a slow start, indicating an increase in photosynthetic efficiency after the transition. Others maintain consistent growth rates, suggesting stable energy production from both stored reserves and photosynthesis during the entire early developmental stage. These differences are likely to be tied to genetic factors that regulate leaf area development, photosynthetic machinery—particularly chloroplast formation—and other physiological traits that influence a plant's photosynthetic efficiency (Ha et al. 2017). The heterotrophic-to-autotrophic transition has a significant impact on early plant growth. Differences in the timing, efficiency, and capacity of plants to transition to autotrophic growth are key drivers of biomass accumulation patterns during early development. Further research is needed to understand these dynamics across genotypes and the mechanisms critical for optimizing growth strategies in agricultural settings, as plants with more efficient transitions may be better suited for specific environments or cultivation practices.

In parallel with the shift to autotrophic growth, root system development and biomass allocation are vital for supporting plant growth (Shipley and Meziane 2002). During this phase, a significant portion of resources is directed towards root growth to establish an efficient system for water and nutrient uptake. This allocation strategy ensures a robust root system before extensive shoot development, with the balance between root and shoot growth carefully regulated according to environmental conditions, particularly nutrient availability (Poorter et al. 2012). Plants in nutrient-limited conditions tend to allocate more resources towards root development. The ability to develop an extensive root system rapidly can provide a competitive advantage, especially in resource-limited environments, as it allows plants to explore deeper soil layers. Root architecture, including depth and branching patterns, directly influences a plant's ability to access water and nutrients (Hodge et al. 2009), further supporting the transition to autotrophic growth. Unfortunately, root traits were not measured in the current study, and future research should pay attention to the roles of biomass allocation and root development in rice's early growth.

5 | Conclusion

A two-year field experiment focusing on the early growth stages was conducted using 90 rice genotypes. The results revealed substantial variation in early growth among the genotypes assessed, providing critical insights into the genetic potential for early vigor in rice. We identified five distinct growth patterns, with the "Consistently Rapid" and "Early Surge" groups demonstrating promising potential for enhanced early growth, which could be pivotal in offsetting yield losses typically associated with shorter growth periods. Our findings also challenge the conventional notion of a constant RGR during the early growth stage, highlighting its dynamic nature and strong correlation with NAR. These insights present valuable opportunities for breeding programs to focus on genotypes with favorable growth dynamics, ultimately enhancing early vigor and optimizing yield in simplified rice cultivation systems such as direct seeding.

Author Contributions

Y.F. conducted the investigation with assistance from Z.C. D.X. led the research design, carried out data analysis with inputs from Y.F., and drafted the manuscript. X.L. organized and revised the manuscript. Y.F., Z.C., X.Y., K.C., J.H., and S.P. contributed significant revisions. All authors reviewed and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Climate conditions during the experimental period. **Figure S2:** Mean and variability of biomass accumulation in 90 rice accessions at three different growth stages. **Figure S3:** Fitted growth curves based on the power model for data collected from 90 rice accessions. **Figure S4:** Improving the fit of the growth model by more frequent early sampling, based on data from an extensive 2022 field experiment. **Figure S5:** Instantaneous growth rate derived from power-law models. **Figure S6:** Pairwise correlations between relative growth rate (RGR) and its components. **Figure S7:** Pairwise correlations between size-standardised relative growth rate (sRGR) and its components. **Table S1:** List of rice materials used in the current study. **Table S2:** Descriptive statistics for growth traits.