

Growth responses of *P. yunnanensis* seedlings to exogenous GA and PAC

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Abstract

Pinus yunnanensis Franch. is a native tree species endemic to south-western China, possessing significant ecological and economic value. To investigate the effects of exogenous hormones on biomass accumulation and heterotrophic growth in *P. yunnanensis* seedlings, this study used one-year-old *P. yunnanensis* seedlings and established three treatment groups: a distilled water control (CK), Gibberellic Acid (GA) and Paclobutrazol (PAC). Root, stem and leaf biomass were measured at regular intervals in March, June, September and December. Pearson's correlation and Mantel's test were employed to systematically analyze biomass dynamics, organ heterotrophic growth and trait associations. The results showed that biomass continued to increase across all treatment groups throughout the growing season; GA significantly promoted biomass accumulation in all organs, whilst PAC inhibited the growth of above-ground organs. As growth progressed, organ growth shifted from isometric to allometric patterns, with the greatest inter-group differences observed in September; GA enhanced the coordination of organ growth, whilst PAC reduced it. Biomass exhibited temporal synchronization, with significant positive correlations among organ biomasses in March and December; in June, correlations were weaker and some indicators showed negative correlations, marking a critical period for the transition in growth strategies; Mantel analysis indicated that PAC exhibited the strongest overall association with biomass, followed by GA, with CK showing the weakest association; different hormonal treatments markedly altered the correlation patterns among organ biomasses. This study elucidated the characteristics of seedling growth changes under hormonal influence, providing a reference for the cultivation of high-quality, robust seedlings.

1 Introduction

Pinus yunnanensis Franch. is a native conifer species endemic to south-western China, playing a significant role in the construction of the ecological barrier in the upper reaches of the Yangtze River and in the restoration of degraded mountain vegetation; its adaptability to karst habitats has been verified (Zheng et al., 2024). It plays an irreplaceable ecological role in soil and water conservation and biodiversity protection, whilst also possessing significant economic value in areas such as rosin extraction and timber processing (Sun et al., 2023). The seedling stage, being the critical phase in the life cycle of *P. yunnanensis* with the greatest plasticity in growth strategies, sees its biomass accumulation efficiency and inter-organ growth coordination directly determine seedling quality, which in turn influences afforestation survival rates and subsequent stand productivity (Lu et al., 2025). However, in the practice of artificial cultivation, *P. yunnanensis* seedlings often encounter issues such as the imbalance between the growth of above-ground parts and root development (Ma et al., 2018) and the irrational biomass structure. These problems result in weak stress resistance of the seedlings and poor forestation effects (Liu et al., 2022). Therefore, it is still necessary to explore scientific and efficient growth regulation techniques.

As a key functional trait reflecting the accumulation of plant biomass and the capacity for resource utilization, the rhythms of biomass accumulation, structural characteristics of biomass, and

relationships of heterotrophic growth between organs provide crucial insights into plant growth strategies and environmental adaptability (Maes et al., 2020; Song et al., 2024). According to the optimal allocation hypothesis (Monson et al., 2022), plants prioritize the allocation of resources to organs acquiring limiting resources in order to maintain the highest growth rate; meanwhile, the theory of heterotrophic growth reveals the intrinsic relationship between plant morphological traits and individual size (Tumber-Dávila et al., 2022), providing a key theoretical framework for understanding organ growth coordination. Resonance between organ growth and biomass accumulation plays a significant role in plants (Gan et al., 2019), exogenous hormones, as highly efficient signal molecules regulating plant growth and development (Zhang et al., 2023), can precisely intervene in cell division and elongation by modulating the balance of endogenous hormones, thereby altering the transport and distribution of photosynthetic products (Lee et al., 2024; Liu et al., 2023) and consequently reshaping the relationship between biomass accumulation patterns and organ growth. This is consistent with Liping Shan 'enemy release hypothesis', which proposes the reallocation of metabolites from the defense system to a state of enhanced growth (Shan et al., 2023). This regulatory approach has been widely applied in the seedling propagation of coniferous species such as *Pinus massoniana* Lamb and *Cunninghamia lanceolata* Hook, yielding significant results.

Gibberellic acid (GA) and paclobutrazol (PAC) are the two most widely used plant growth regulators in the propagation of coniferous tree species; their mechanisms of action are complementary: GA promotes cell elongation, accelerates stem and leaf growth and increases photosynthetic area, thereby enhancing the efficiency of photosynthetic product accumulation (S. Li et al., 2024); PAC, acting as a GA synthesis inhibitor (Wu et al., 2024) suppresses above-ground growth, promotes the transport of carbohydrates to the root system, enhances root growth, and improves the root/shoot and stress tolerance of seedlings (Ma et al., 2018). In recent years, researchers both domestically and internationally have conducted extensive studies on the regulation of conifer seedling growth by exogenous hormones, confirming the significant effects of GA and PAC on biomass accumulation and root development (Pimenta Lange & Lange, 2006). However, existing research still has notable shortcomings: Firstly, most studies focus on phenotypic indicators such as seedling height and stem diameter at ground level, with investigations into biomass remaining limited to the total biomass of individual plants. There is a lack of detailed descriptive statistics on the biomass of organs such as root, stem and leaf, as well as a systematic integration of key auxiliary indicators such as biomass structural characteristics (S. Li et al., 2024); Secondly, heterotrophic growth analysis is largely confined to a single dimension of 'organ versus individual plant', with insufficient attention paid to the heterotrophic growth relationships between organs such as root–stem, root–leaf and stem–leaf (Niklas, 2006), and no dynamic studies spanning multiple seasons have been conducted in conjunction with key growth stages (Wang et al., 2017); Thirdly, research on hormonal regulation in *P. yunnanensis* seedlings remains relatively underdeveloped, consisting mainly of short-term studies focusing on single indicators. There is a lack of systematic comparisons between GA and PAC, and no analysis of coefficient of variation has been conducted to quantify the stability of biomass indicators under hormonal regulation (Dietrich et al., 2024),

making it difficult to draw research conclusions that possess both theoretical value and practical guidance.

Meanwhile, relevant studies have confirmed that, under environmental stress (C. Zhang et al., 2022) or artificial intervention (Guo et al., 2018; C. Zhang et al., 2022), *P. yunnanensis* seedlings adapt to environmental changes by adjusting their biomass allocation, structural characteristics and allometric growth strategies (LeBauer & Treseder, 2008; Song et al., 2024). For example, following pruning, the root system of *P. yunnanensis* seedlings enhance their capacity to absorb water and nutrients by altering morphological characteristics and biomass allocation (Ji et al., 2026; Zhang et al., 2026); furthermore, fertilization with a specific nitrogen-to-phosphorus ratio significantly influences the allometric growth relationships between organs, thereby regulating the growth rhythm of seedlings (He et al., 2022; Wang et al., 2017). This provides important insights into the regulation of biomass and allometric growth in *P. yunnanensis* seedlings by exogenous hormones; however, as hormones act as more direct growth regulators (Müller & Munné-Bosch, 2017), their comprehensive regulatory effects on biomass accumulation, structural characteristics, and inter-organ allometric growth in *P. yunnanensis* seedlings remain unclear.

Accordingly, this study focuses on one-year-old *P. yunnanensis* seedlings, with three treatment groups established: a control group (CK) using distilled water, a 200 mg/L GA treatment, and a 100 mg/L PAC treatment. Through year-round dynamic monitoring, the study conducts a systematic investigation centered on key biomass indicators. The research aims to characterize biomass by determining the mean, standard deviation and coefficient of variation of biomass across different organs for each treatment and at different growth stages; to analyze the dynamics of biomass accumulation, the characteristics of biomass composition (root/shoot, leaf/stem, etc.) the dynamic patterns; to focus on analyzing the heterotrophic growth relationships between organs (root–leaf, root–stem, etc.), growth increments and root system; and, by combining correlation analysis with radar charts of coefficients of variation, to quantify the regulatory effects and mechanisms of exogenous hormones on the biomass and growth characteristics of *P. yunnanensis* seedlings.

The innovative aspects of this study lie in the following: for the first time, it systematically integrates accumulation dynamics, structural characteristics and multidimensional heterotrophic growth relationships to establish a comprehensive analytical framework for the biomass of *P. yunnanensis* seedlings; it overcomes the limitations of existing research on heterotrophic growth by focusing on synergistic growth responses between organs, thereby revealing shifts in growth strategies under hormonal regulation; and through coefficient of variation analysis, it quantifies the stability of hormonal regulation, providing precise guidance for seedling cultivation practices. The findings not only enrich the theoretical framework of plant growth regulation by contributing to research on the effects of hormones on seedling biomass and heterotrophic growth in coniferous species, and fill a gap in research on the systemic regulation of exogenous hormones in *P. yunnanensis* seedlings, but also enable the identification of hormone treatment protocols suitable for different seedling-rearing scenarios. This provides crucial theoretical support and technical guidance for the large-scale cultivation of high-quality,

robust *P. yunnanensis* seedlings, ecological restoration, and the high-quality development of the forestry industry in the south-western region.

2 Materials and Methods

2.1 Overview of the Experimental Site

The experiment was conducted in the Greenhouse at Southwest Forestry University in Kunming, Yunnan Province (25°04'00" N, 102°45'41" E). The site is situated at an altitude of approximately 1,945 m and exhibits the typical characteristics of a low-latitude subtropical plateau monsoon climate. The climatic conditions are characterized by: ample sunshine throughout the year, with a cumulative sunshine duration of 2,200 hours; a small annual temperature variation, with the annual average temperature maintaining around 17.1°C, of which the average temperature in the hottest summer month is 19°C and in the coldest winter month is 7.6°C; Annual rainfall is approximately 700–1,000 mm, with precipitation concentrated during the rainy season from May to October. The dry season, from November to April of the following year, sees relatively little rainfall, exhibiting distinct seasonal patterns.

2.2 Experimental Materials

2.2.1 Source of Seed Material

The *P. yunnanensis* seeds used in this experiment were collected from the clonal seed orchard at the National *P. yunnanensis* Elite Seed Base in Midu County, Dali Prefecture, Yunnan Province. During collection, only vigorous female trees with excellent characteristics were selected. Within the elite seed base, healthy cones that had set seed in the current year and were well-developed were selected. After collection, the cones were labelled with identification numbers and transported to the laboratory. Following natural air-drying, high-quality seeds with plump grains and uniform size were carefully selected. Seed disinfection involved soaking the seeds in a 0.5% potassium permanganate solution for 1 hour, followed by repeated rinsing with distilled water and soaking in a constant-temperature water bath at 25°C for 24 hours. Sowing is then carried out, followed by covering the seeds with pine needles to retain moisture. A plastic arch is erected and covered with plastic sheeting, and water management and weed control are carried out in accordance with standard seedling-rearing procedures; following sowing, the seeds were covered with pine needles to retain moisture, and a plastic arch was erected and covered with plastic sheeting. Water management and weed control were carried out in accordance with standard seedling propagation procedures. Once the seedlings had completed the germination stage, the seedlings, which had been growing for approximately 100 days, were transplanted into custom-made pots (dimensions: height 32 cm, base diameter 18 cm). The growing medium was prepared using a volume ratio of 3:1 humus to red soil. Throughout the experiment, all seedlings were subjected to identical management practices to ensure consistent environmental conditions and maximize potential interference from external factors on the experimental results.

2.2.2 Exogenous Hormone Treatment

Based on the optimal concentration determined in preliminary trials, *P. yunnanensis* seedlings of uniform growth were selected for exogenous hormone treatment trials. As shown in Table 1, the trial comprised three treatments. Foliar spraying was carried out using a hand-held sprayer, with treatments applied every five days for a total of six consecutive applications. During spraying, the degree of atomization was controlled to ensure that the surfaces of the stem and leaf were uniformly moistened (to the extent that a film of water formed on the leaf surface but no droplets fell). The experiment employed a completely randomized block design, with three replicates per treatment. Each replicate comprised three sub-plots, making a total of nine sub-plots. One hundred seedlings were planted in each sub-plot, resulting in a total of 900 seedlings used in the experiment.

Table 1
Concentration settings for exogenous hormone treatment

Treatment group	GA concentration(mg/L)	PAC concentration(mg/L)
CK	0	0
GA	200	0
PAC	0	100

2.3 Biomass measurement

Six seedlings were randomly selected from each treatment group (18 seedlings in total per trial), The seedlings were excavated using the whole-plant harvesting method, and the fresh weight of organs such as root, stem and leaf was determined using a precision electronic balance (accuracy 0.001 g). After labelling, the samples were placed in envelopes and subjected to a 30-minute fixation treatment at 105°C, followed by drying at 80°C until constant weight was achieved, thereby obtaining the final values for each organ. The following biomass parameters were calculated based on the biomass data: aboveground biomass (stem + leaf), photosynthetic organ biomass (leaf), non-photosynthetic organ biomass (stem + root), and individual plant biomass (root + stem + leaf). The biomass allocation ratio was defined as the ratio of a given organ’s biomass to the individual plant biomass.

To elucidate the biomass composition characteristics of *P. yunnanensis* seedlings and to clarify the relationships between material allocation and resource allocation strategies among underground and above-ground parts, as well as between photosynthetic and non-photosynthetic organs, under different exogenous hormone treatments, structural indices such as biomass ratios between organs were calculated based on measured biomass data for the root, stem and leaf.

Furthermore, to quantify the stability of biomass indicators across treatments, the coefficient of variation (CV) was calculated as (standard deviation / mean) × 100%. A lower CV value indicates greater stability of biomass traits under that treatment.

The calculation formulas for indicators related to biomass structural characteristics are as follows:

$$\text{Stem/Root} = W_S/W_R$$

$$\text{Leaf/Stem} = W_L/W_S$$

$$\text{Leaf /Root} = W_L/W_R$$

$$\text{Root/Shoot} = W_R/W_S$$

$$P/NP = W_L/(W_R+W_S)$$

In the equation: W represents biomass; W_R , W_S and W_L represent root, stem and leaf biomass (g) respectively; P/NP represents the ratio of photosynthetic to non-photosynthetic organs.

2.4 Statistical Analysis of Correlations

To elucidate the relationships between the various indicators and seedling growth traits, A heat map of the network has been created. This included conducting Pearson correlation analyses using SPSS 27.0 to assess the linear relationships between the indicators and seedling growth traits, as well as utilizing the Mantel test to evaluate the overall correlations between the treatments, indicators and seedling growth traits. The Mantel test calculates the correlation coefficient (r) based on a difference matrix; its values range from -1 to 1 . A value of $r > 0$ indicates a positive correlation, with a higher value indicating a stronger correlation; a value of $r < 0$ indicates a negative correlation, with a larger absolute value indicating a more significant negative correlation; when $r = 0$, it indicates that there is no obvious linear correlation between the matrices. This test employs a permutation test to assess statistical significance, typically using a significance level of $p < 0.05$.

3 Results

3.1 Effects of exogenous hormone treatment on the dynamic of biomass accumulation in *P. yunnanensis* seedlings

All biomass parameters exhibited distinct seasonal variations, with the total biomass of individual organs and plants rising continuously from March to December. The aboveground parts served as the primary organs of accumulation, with accumulation rates following the order: stem > leaf > root.

The GA-treated groups exhibited the highest biomass across all components and time periods: total plant biomass (Fig. 1A) increased significantly, with this advantage becoming more pronounced in the later stages; root biomass (Fig. 1B) was significantly promoted by GA, with the effect being particularly pronounced from September to December, thereby improving root development and nutrient uptake; stem biomass (Fig. 1C) and leaf biomass (Fig. 1D) increased significantly, with GA enhancing vegetative

growth by promoting cell elongation and division; aboveground biomass (Fig. 1E) increased in tandem, whilst non-photosynthetic biomass (Fig. 1F) accumulated, thereby enhancing overall productivity.

PAC treatment significantly inhibited biomass accumulation: stem biomass (Fig. 1C) and leaf biomass (Fig. 1D) were most markedly suppressed, peaking in June; PAC merely slowed the growth rate, whilst total biomass individual (Fig. 1A), root biomass (Fig. 1B), aboveground biomass (Fig. 1E) and non-photosynthetic biomass (Fig. 1F) continued to increase slowly. Biomass under the CK treatment fell between the two, with steady growth that was significantly lower than that of GA.

3.2 Effects of exogenous hormone treatment on the biomass composition of *P. yunnanensis* seedlings

Figure 2. illustrates the dynamic regulation of biomass structural characteristics in *P. yunnanensis* seedlings following exogenous hormone treatment. Each structural parameter exhibited significant changes across growth stages. Notably, the stem/root (Fig. 2A) was significantly higher in the GA treatment than in the CK and PAC treatments, indicating that GA significantly increased the relative proportion of stem biomass and conferred a distinct structural advantage to the above-ground vegetative organs, whereas the PAC treatment exhibited the lowest stem/root and inhibited stem growth; The leaf/stem (Fig. 2B) was highest in the GA treatment, indicating a greater proportion of leaf structure, whilst the PAC treatment had the lowest ratio, with a relatively lower proportion of photosynthetic organ structure; the leaf/root (Fig. 2C) was significantly highest in the GA treatment, exhibiting a structural characteristic dominated by above-ground photosynthetic organs, whereas the PAC treatment had the lowest ratio, reflecting a structural pattern dominated by the underground root system; The root/shoot (Fig. 2D) was significantly highest in the PAC treatment, with a significantly increased proportion of underground structures, whilst it was lowest in the GA treatment, with a higher proportion of above-ground structures; P/NP (Fig. 2E) showed a higher proportion of photosynthetic organ structure in the GA treatment, a higher proportion of non-photosynthetic organ structure in the PAC treatment, and the CK treatment falling between the two; Overall, the GA treatment resulted in a biomass structure dominated by the aboveground parts with a prominent proportion of photosynthetic organs, whilst the PAC treatment resulted in a biomass structure dominated by the root system with a prominent proportion of non-photosynthetic organs. Structural differences between the treatments gradually emerged between March and June, peaked in September, and stabilized by December.

3.3 The Regulation of Variation in Biomass Traits of *P. yunnanensis* Seedlings by Exogenous Hormone Treatment

Figure 3. illustrates the dynamic changes in the coefficients of variation for various biomass traits of *P. yunnanensis* seedlings under CK, GA and PAC treatments at four time points (March, June, September and December), reflecting the regulatory effects of exogenous hormones on the stability of biomass traits; In March (Fig. 3A), the coefficients of variation for biomass traits under the GA treatment were

generally high, indicating greater dispersion and lower stability of these traits, whereas the coefficients of variation for the CK and PAC treatments showed little difference, with relatively stable trait expression. By June (Fig. 3B), differences in the coefficients of variation between treatments gradually became apparent; notably, the coefficient of variation for root biomass in the CK treatment increased significantly, GA continued to exhibit high variability in aboveground biomass traits, whilst PAC showed increased variability and reduced stability in root biomass traits. By September (Fig. 3C), differences in coefficients of variation between treatments reached a peak; the coefficient of variation for aboveground biomass traits under GA remained at a high level, whilst those for root and stem biomass traits under PAC rose significantly, with CK's overall variability lying between the two. By December (Fig. 3D), the differences in variability between treatments had declined slightly, but the overall pattern had stabilized. CK's biomass trait variability had decreased somewhat, whilst the trait variability patterns exhibited by GA and PAC remained constant, demonstrating that exogenous hormones exert a long-term regulatory effect on the stability of biomass traits in *P. yunnanensis* seedlings.

3.4 Effects of exogenous hormone treatment on the allometric growth relationships among organs of *P. yunnanensis* seedlings

After logarithmic transformation, the biomass of all six organ groups showed a significant linear correlation ($p < 0.05$), with good SMA fitting; the allometric growth indices and coefficients of determination varied significantly with growth duration and treatment.

As the growth period extended from March to December, root–stem biomass (Fig. 4A, 5A, 6A, 6A) exhibited balanced, isometric growth in the early stages of CK, with allometric differentiation occurring in the middle and late stages; In contrast, root growth accelerated in the later stages of the PAC treatment, exhibiting distinct allometric growth. Stem–leaf biomass (Fig. 4B, 5B, 6B, 7B) showed overall isometric growth in both the CK and PAC treatments as growth progressed, with stable growth ratios.

With regard to root–leaf biomass (Fig. 4C, 5C, 6C, 7C), GA effectively promoted the growth of aboveground organs during the later stages of growth, whilst natural growth in the CK treatment exhibited isokinetic characteristics. In terms of root–aboveground biomass (Fig. 4D, 5D, 6D, 7D), as seedlings matured, GA exhibited a high degree of growth synergy, whereas the coordination of organ growth in the PAC treatment gradually decreased.

Regarding biomass between aboveground organs (Fig. 4E, 5E, 6E, 7E), PAC and GA exhibited heterotrophic growth in the early and middle stages, gradually stabilizing in the later stages. Finally, concerning stem-to-aboveground biomass and biomass of photosynthetic versus non-photosynthetic organs (Fig. 4F, 5F, 6F, 7F), GA increased stem growth rates in the later stages, exhibiting a typical heterotrophic growth pattern.

In March, all organs in each treatment group exhibited uniform growth, with no significant differences; by June, hormonal regulation became apparent, with GA enhancing above-ground growth and PAC accelerating root growth; by September, differences between treatments reached their peak; by

December, all organs exhibited growth dominance in a single organ, with GA showing the strongest synergistic effect, PAC the weakest, and CK an intermediate effect.

3.5 Correlation analysis of biomass indicators of *P. yunnanensis* seedlings under exogenous hormone treatment

Biomass variables exhibited temporal synchrony and trait synchrony. Overall, there was a positive correlation between biomass trait samples collected at the same time point, as evidenced by the numerous red circles along the diagonal of the correlation matrix. Positive correlations were particularly pronounced among variables at 3 and 12 months, suggesting synchrony in biomass development during the early and late stages of growth. More specifically, at 12 months, significant positive correlations were observed between root biomass, stem biomass, leaf biomass, aboveground biomass and individual biomass, indicating that organ development and the plant as a whole tend to be consistent in terms of biomass growth. On the other hand, some combinations of variables collected at 6 months showed weaker correlations or even negative correlations with other time points, suggesting that 6 months may represent a transitional point in biomass distribution. As shown in the Mantel network, PAC exhibited the highest total number of connections with biomass traits, followed by GA, whilst the level of association for CK was relatively low.

4 Discussion

4.1 The effects of different treatment methods on biomass accumulation and structural characteristics

Previous studies have shown that chronological age is a major factor influencing the accumulation and structural characteristics of biomass and nutrients, with significant differences observed between different organs in terms of biomass and nutrient storage (Yang et al., 2010). Other studies have also indicated that various exogenous hormones can influence these outcomes; the results of this study demonstrate that the effects of exogenous hormones on biomass are consistent with the aforementioned patterns.

In this study, the different treatments significantly altered the rate of biomass accumulation and the organ allocation ratio in seedlings, exhibiting overall characteristics of 'seasonal differentiation, above-ground preference, and significant differences between treatments. Throughout the entire growth cycle, seedling biomass exhibited a continuous upward trend. Under the GA treatment, the biomass of all organs and individual plants underwent a rapid accumulation phase from June to September, with enhanced GA signal(Wang et al., 2025), significantly exceeding that of the CK and PAC treatments; whereas the PAC treatment, although exhibiting a certain promotional effect in the early stages, showed a marked slowdown in growth after September. This is consistent with the growth rhythms of most

temperate coniferous seedling species(Landuyt et al., 2019; Yan et al., 2025), indicating that this stage is a critical period for carbon assimilation(Chen et al., 2024; Petit et al., 2016), substance synthesis and organ development. Previous studies have found that dynamic CHH methylation regulates the dormancy process and promotes bud break by negatively regulating the expression of hormone signal genes such as IAA, GA and CK (Chen et al., 2026). In conjunction with the results of this study, this is consistent with the functions of gibberellin in promoting cell elongation (S. Li et al., 2024) and enhancing photosynthetic carbon assimilation(Chen et al., 2024), whilst also validating the negative regulatory mechanism whereby PAC inhibits GA synthesis and thereby restricts above-ground growth(Y. Zhang et al., 2022). The differences between treatment rooms gradually widened over time, indicating that exogenous regulation can improve plant photosynthesis and promote plant growth and development by altering the allocation of resources (Liu et al., 2023; Xu et al., 2012). Furthermore, exogenous hormones significantly altered the structural characteristics of seedling biomass; GA treatment significantly increased the stem/root, leaf/stem and proportion of the aboveground biomass, resulting in an aboveground-dominant configuration; in contrast, PAC treatment resulted in a higher root/shoot, indicating a root-dominant structural pattern. This structural differentiation reflects the hormone's targeted regulation of seedling growth strategies.

4.2 The regulatory effects of different treatments on the seasonal dynamics of biomass

The effects of different treatments on seedling biomass exhibited distinct temporal patterns, consistent with the dynamic trends observed between March and December. Differences were minimal in the early stages but rapidly widened upon entering the rapid growth phase. GA treatment significantly increased the proportion of the above-ground structure, demonstrating a growth strategy characterized by 'rapid growth, uniformity and prioritization of the above-ground parts'(Pimenta Lange & Lange, 2006), which is conducive to the rapid development of robust seedlings and improved population uniformity during the seedling rearing stage(Wang et al., 2020). To cope with drought, some plants typically redirect more biomass to the root to facilitate water uptake; for example, AM fungi promote plant growth and stabilize growth rates by enhancing nutrient and water absorption during drought periods(Tang et al., 2024). PAC treatment exhibits similar functions, manifesting as a distribution pattern characterized by "root-priority, robust growth and enhanced stress tolerance". Although biomass accumulation is relatively moderate, the proportion of biomass allocated to the root is higher, which may exacerbate fluctuations in carbon allocation between photosynthetic and non-photosynthetic organs in the aboveground parts(Huang et al., 2023; Jevon & Lang, 2022), making it suitable for use in adverse environments or during the later stages of seedling cultivation. The control group had the lowest biomass and the greatest variation in traits, reflecting the fact that, under natural conditions, seedling growth is significantly influenced by the environment and exhibits poor uniformity.

4.3 Differences in the response of inter-organ growth relationships to treatment

Allometric growth reflects the intrinsic trade-offs in resource allocation among plant organs. Based on the allometric growth results from this study, it is evident that the logarithmically transformed biomass of the various organs exhibits a significant linear correlation ($p < 0.05$) with a high SMA fit, indicating that organ growth in *P. yunnanensis* seedlings follows a stable allometric pattern and is significantly regulated by exogenous hormones.

The allometric relationships between organs are sensitive to treatment responses, with the 'root–shoot' and 'root–leaf' allometric relationships serving as key indicators for evaluating seedling growth strategies and resource allocation patterns(S. Y. Li et al., 2024). GA treatment significantly enhanced growth synergy between organs, resulting in more stable allometric relationships; PAC treatment exhibited relatively lower synergy, but a higher proportion of root biomass; The results indicate that GA significantly promotes biomass accumulation in all plant components, particularly during the later stages of growth(Liu et al., 2018; Wu et al., 2024), whereas paclobutrazol inhibits plant growth. The control group exhibited the greatest fluctuations in heterotrophic growth ratios, suggesting that seedling growth under natural conditions is more susceptible to environmental influences(Jin et al., 2022). Overall, exogenous regulation can achieve the targeted shaping of seedling growth patterns by altering the trajectories of heterotrophic growth between organs.

4.4 Correlations between biomass traits and growth synchrony

Consistent with the results of the correlation analysis, the analysis revealed that the biomass traits of *P. yunnanensis* seedlings exhibit significant 'temporal synchrony and trait synergy (Staples et al., 2022)'. Organ biomass showed a strong positive correlation during the same period, with the most pronounced correlation observed between the early growth stage (March) and the late growth stage (December), indicating that overall growth in seedlings is highly synchronized during the early and stable phases(Dietrich et al., 2024). Correlations were weaker in June, with some combinations showing negative correlations, representing a "transitional node for the shift in resource allocation strategies". Hormone treatments can enhance the associations between traits, with "PAC having the strongest effect, followed by GA, and CK having the weakest", indicating that exogenous hormones (particularly PAC) can enhance the inter-trait correlations and the ability to integrate environmental responses(Maes et al., 2020). Overall, this indicates that *P. yunnanensis* seedlings achieve efficient resource allocation through 'trait synergy, temporal synchronization, and treatment-dependent network regulation' (Zou et al., 2020), reflecting the adaptive growth mechanisms of coniferous species under artificial control.

Overall, exogenous supplementation of plant hormones can significantly enhance activity(Zhang et al., 2021), enabling the targeted regulation of growth strategies in *P. yunnanensis* seedlings by altering 'biomass accumulation rates, allocation patterns, phenotypic variation, allometric growth trajectories and trait synergies.

The findings of this study provide a theoretical basis and technical support for the large-scale production of high-quality, robust seedlings, the regulation of biomass accumulation, and optimization of organ

structure.

5 Conclusion

This study investigated the regulatory effects of exogenous gibberellic acid and paclobutrazol on the dynamics of biomass accumulation and the patterns of heterotrophic growth among organs in one-year-old *P. yunnanensis* seedlings. The results showed that both exogenous hormones significantly influenced the biomass accumulation process and growth patterns of the seedlings, with biomass in all treatments exhibiting a continuous upward trend over the growth period. The gibberellic acid treatment significantly promoted biomass accumulation in all organs, resulting in more vigorous overall growth of the seedlings; whereas the paclobutrazol treatment exerted a marked inhibitory effect on above-ground growth, resulting in a relatively slower overall rate of biomass accumulation. As the growth process progressed, the growth patterns among the seedling organs gradually shifted from isometric to heterometric growth, with the differences between treatments reaching their most pronounced stage in September. Gibberellic acid was able to maintain a high degree of growth coordination among organs, whilst paclobutrazol led to a reduction in this coordination. The biomass traits of *P. yunnanensis* seedlings exhibited distinct temporal synchronization, with June representing a critical juncture for the shift in growth strategy. Exogenous hormones achieve targeted regulation of the growth patterns of *P. yunnanensis* seedlings by modulating the rhythm of biomass accumulation and the trajectories of organ heterotrophic growth. This study elucidates the regulatory mechanisms of exogenous hormones on biomass accumulation and heterotrophic growth in *P. yunnanensis* seedlings, providing a theoretical basis and technical support for the cultivation of robust seedlings and scientific regulation of *P. yunnanensis*.

Declarations

CRedit authorship contribution statement

Feiyun Wang: Writing – original draft, investigation, review & editing, Conceptualization. **Ruilian Li**: Experimental research, data collation. **Nan Shu**: Data organization. **Guangpeng Tang**: Analysis of standards. **Xiangyang Kang**: Resource support, research supervision. **Nianhui Cai**: Research supervision, fundraising, manuscript revision. **Yulan Xu**: Writing – review & editing, supervision, Funding acquisition, Conceptualization.

Declaration 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.

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Data availability

Data will be made available on request.

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Figures

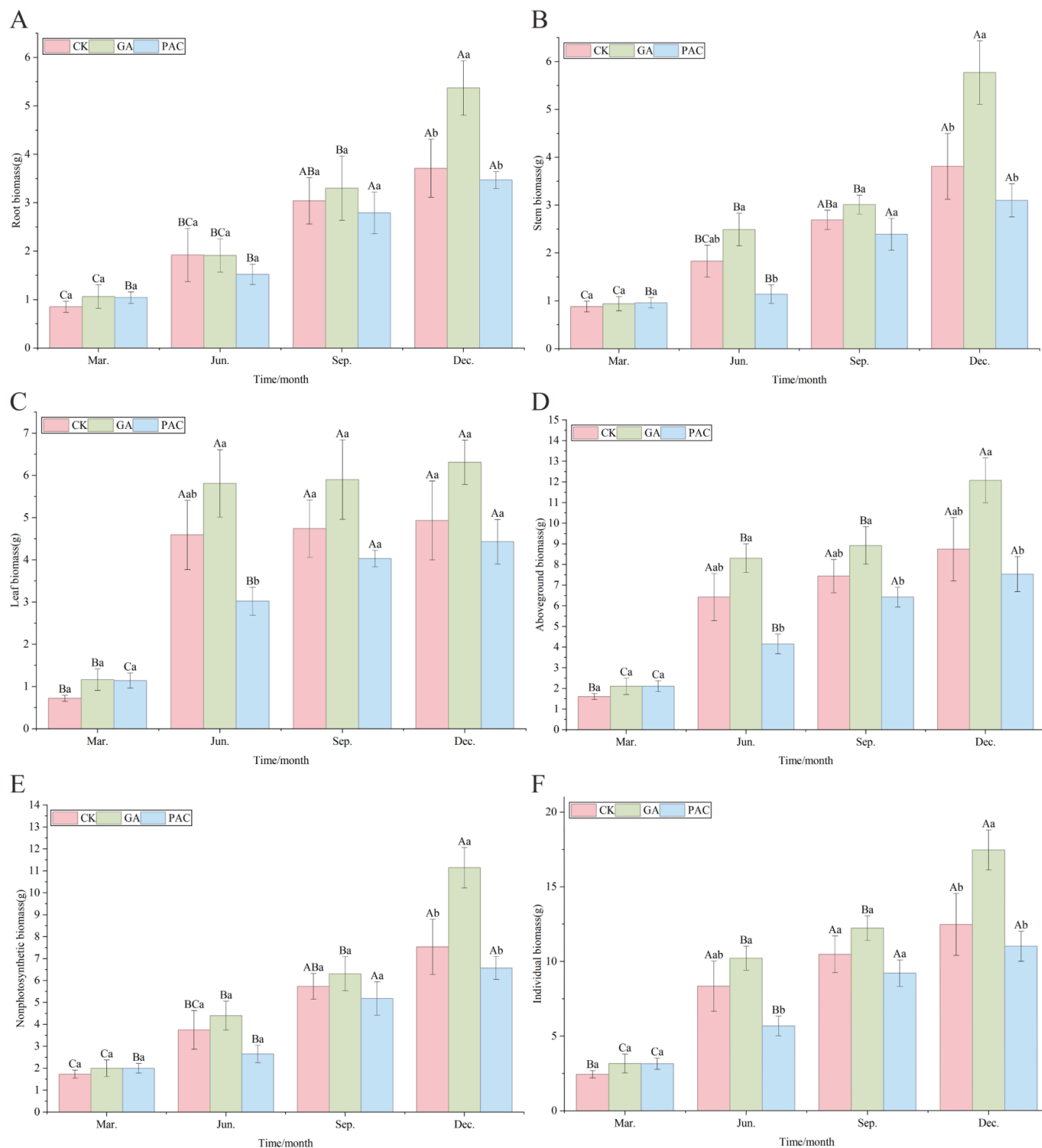


Figure 1

Dynamics of biomass in various organs of *P. yunnanensis* under different exogenous hormone treatments. A root biomass, B stem biomass, C leaf biomass, D aboveground biomass, E non-photosynthetic organ biomass, F individual biomass. CK denotes the distilled water control, GA denotes gibberellic acid treatment, and PAC denotes paclobutrazol treatment. Significant differences between treatment groups at the same time point are indicated by different lowercase letters; significant

differences within the same treatment group at different time points are indicated by different uppercase letters ($p < 0.05$). Data are presented as mean $\pm$ standard error (SE), $n = 6$. A two-way analysis of variance (ANOVA) was performed, with the LSD test used for multiple comparisons. The same applies throughout.

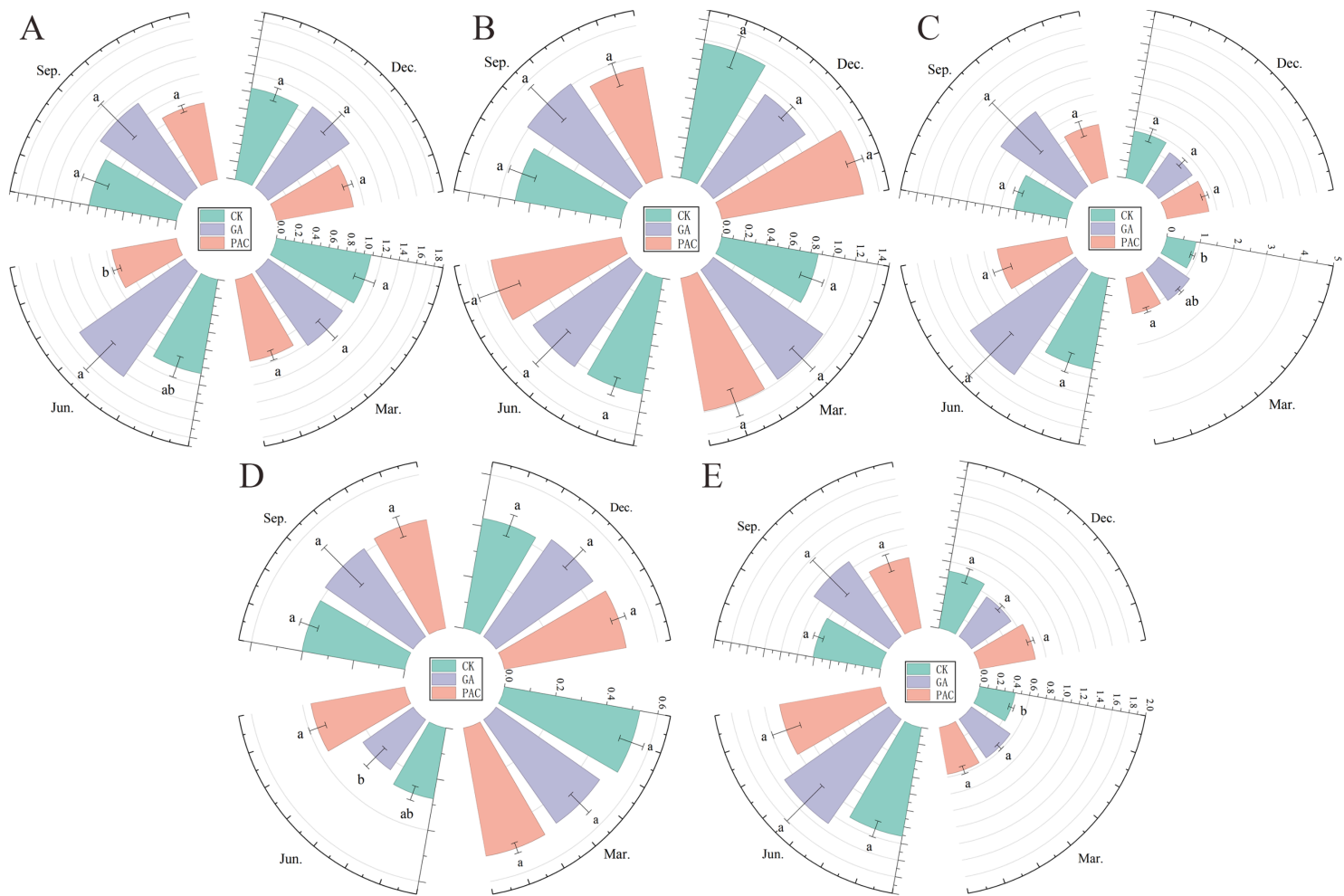


Figure 2

Dynamic changes in the biomass structural characteristics of *P. yunnanensis* seedlings under different exogenous hormone treatments. Stem/Root; B. Leaf/Stem; C. Leaf/Root; D. Root/Shoot; E. P/NP. CK denotes the distilled water control; GA denotes gibberellic acid treatment; PAC denotes paclobutrazol treatment; Mar. denotes March, Jun. denotes June, Sep. denotes September, and Dec. denotes December; different lowercase letters indicate significant differences ($p < 0.05$) between treatments within the same period.

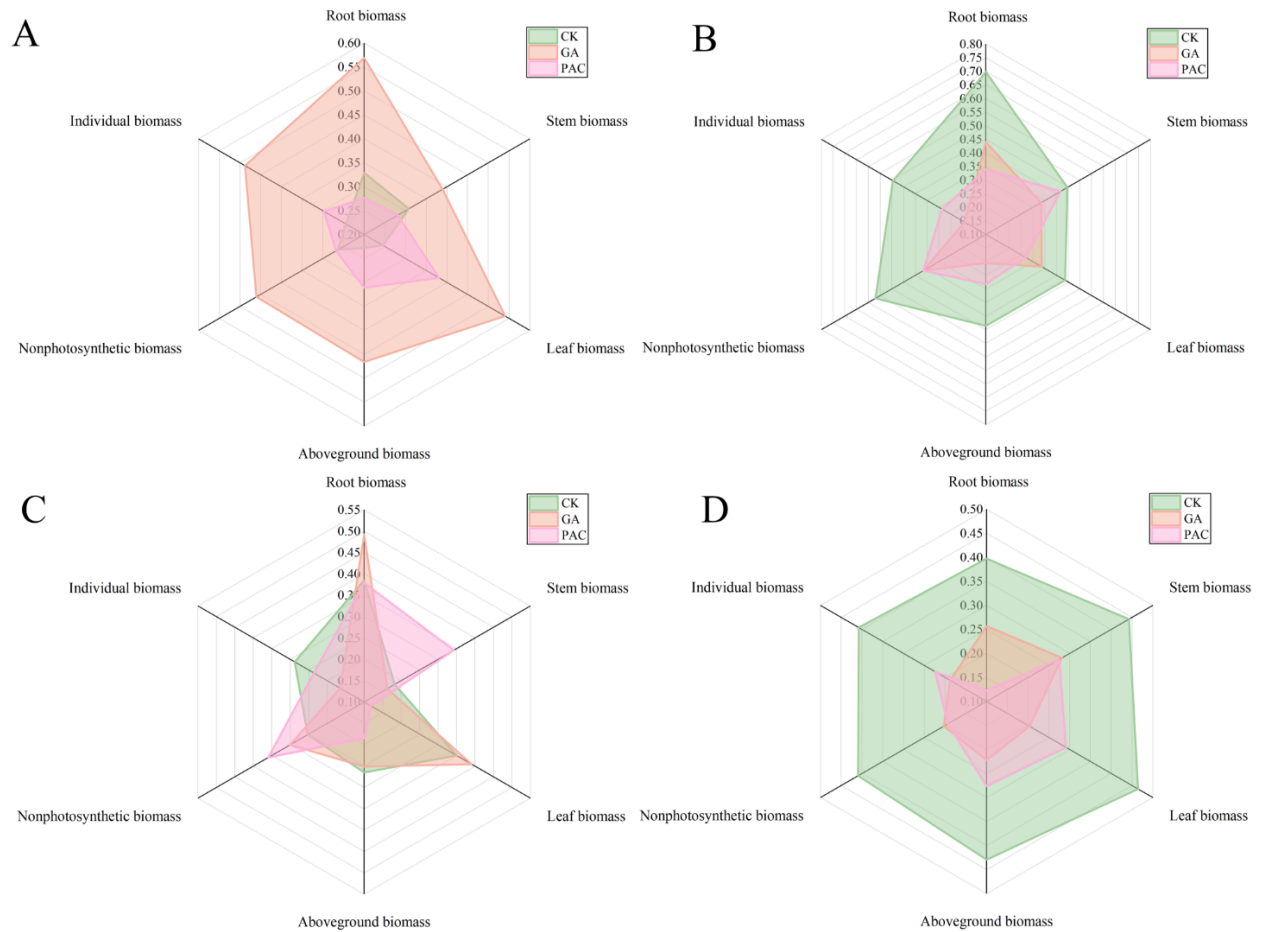


Figure 3

Coefficients of variation in biomass traits of *P. yunnanensis* seedlings under exogenous hormone treatments at different growth stages. A: March; B: June; C: September; D: December. CK denotes the control treatment; GA denotes gibberellic acid treatment; PAC denotes paclobutrazol treatment. The axes in the radar charts represent root biomass, stem biomass, leaf biomass, aboveground biomass, non-photosynthetic biomass and individual plant biomass, respectively.

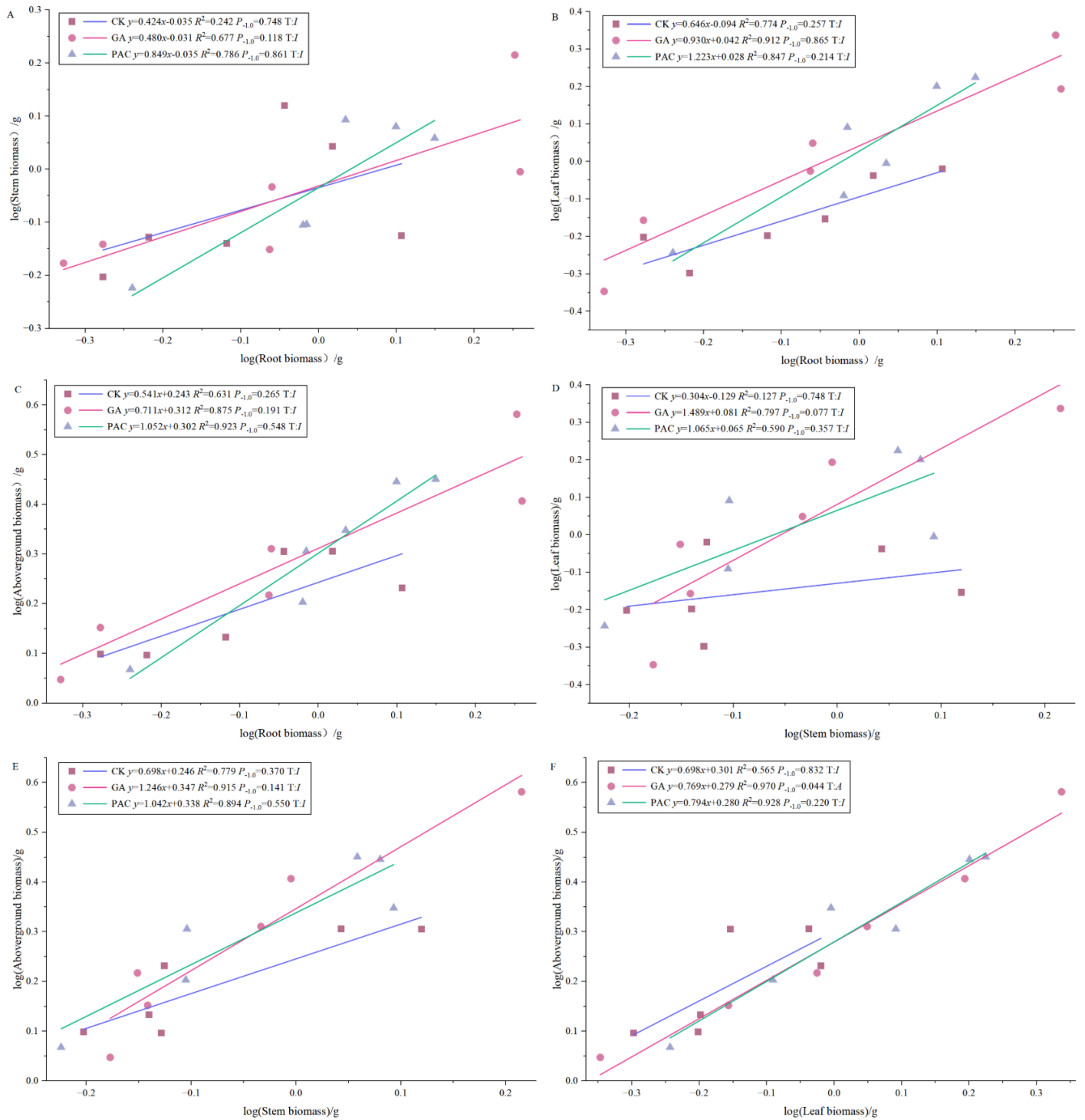


Figure 4

Allometric relationships in March between root biomass and stem biomass (A), root biomass and leaf biomass (B), root biomass and aboveground biomass (C), stem biomass and leaf biomass (D), stem biomass and aboveground biomass (E), and leaf biomass and aboveground biomass (F). The straight lines in the figures represent standardized mean axis (SMA) fitted lines; CK denotes the control treatment, GA denotes gibberellin treatment, and PAC denotes paclobutrazol treatment.

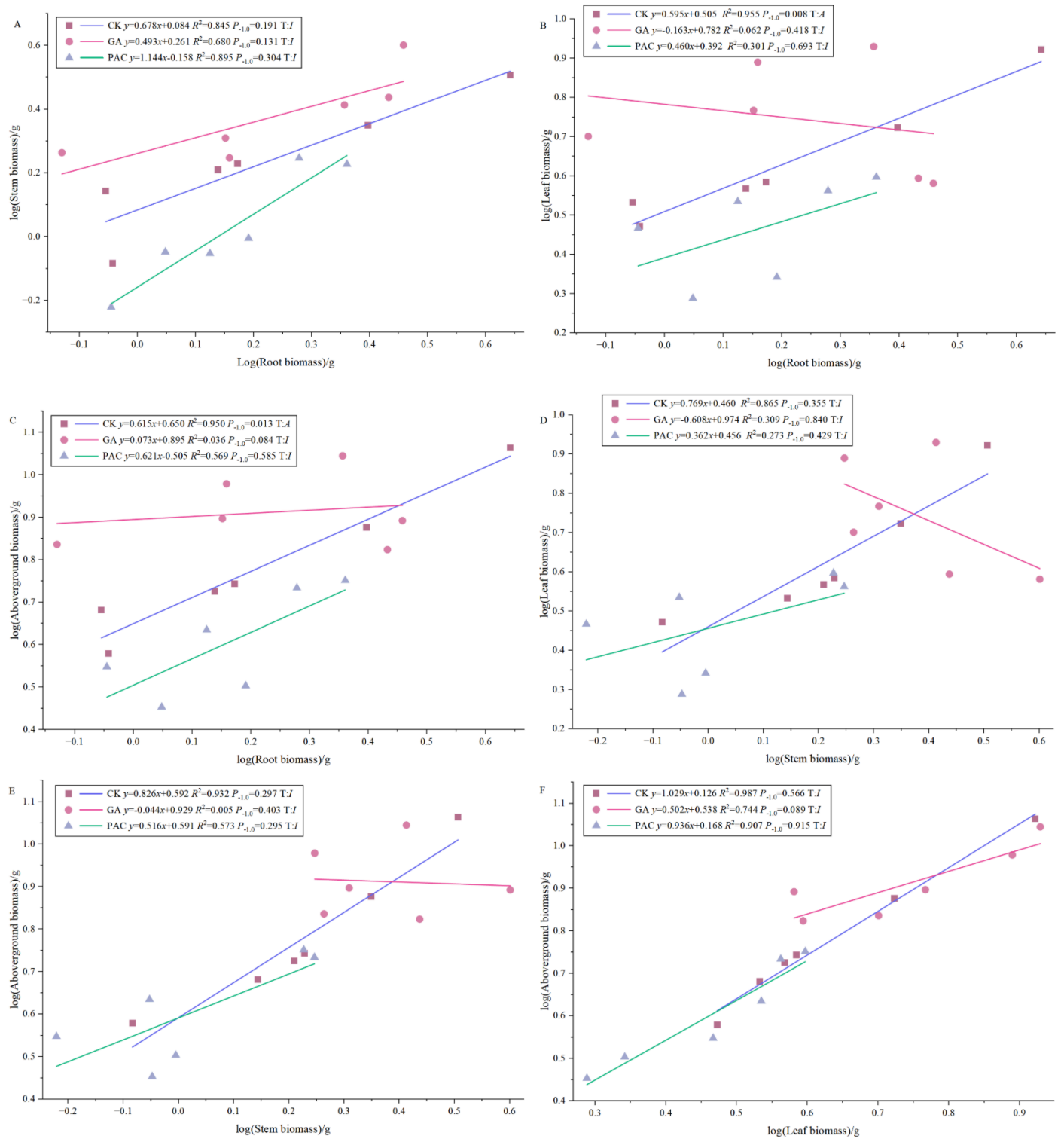


Figure 5

Allometric relationships in June between root biomass and stem biomass (A), root biomass and leaf biomass (B), root biomass and aboveground biomass (C), stem biomass and leaf biomass (D), stem biomass and aboveground biomass (E), and leaf biomass and aboveground biomass (F). The straight lines in the figures represent standardized mean axis (SMA) fitted lines; CK denotes the control treatment, GA denotes gibberellin treatment, and PAC denotes paclobutrazol treatment.

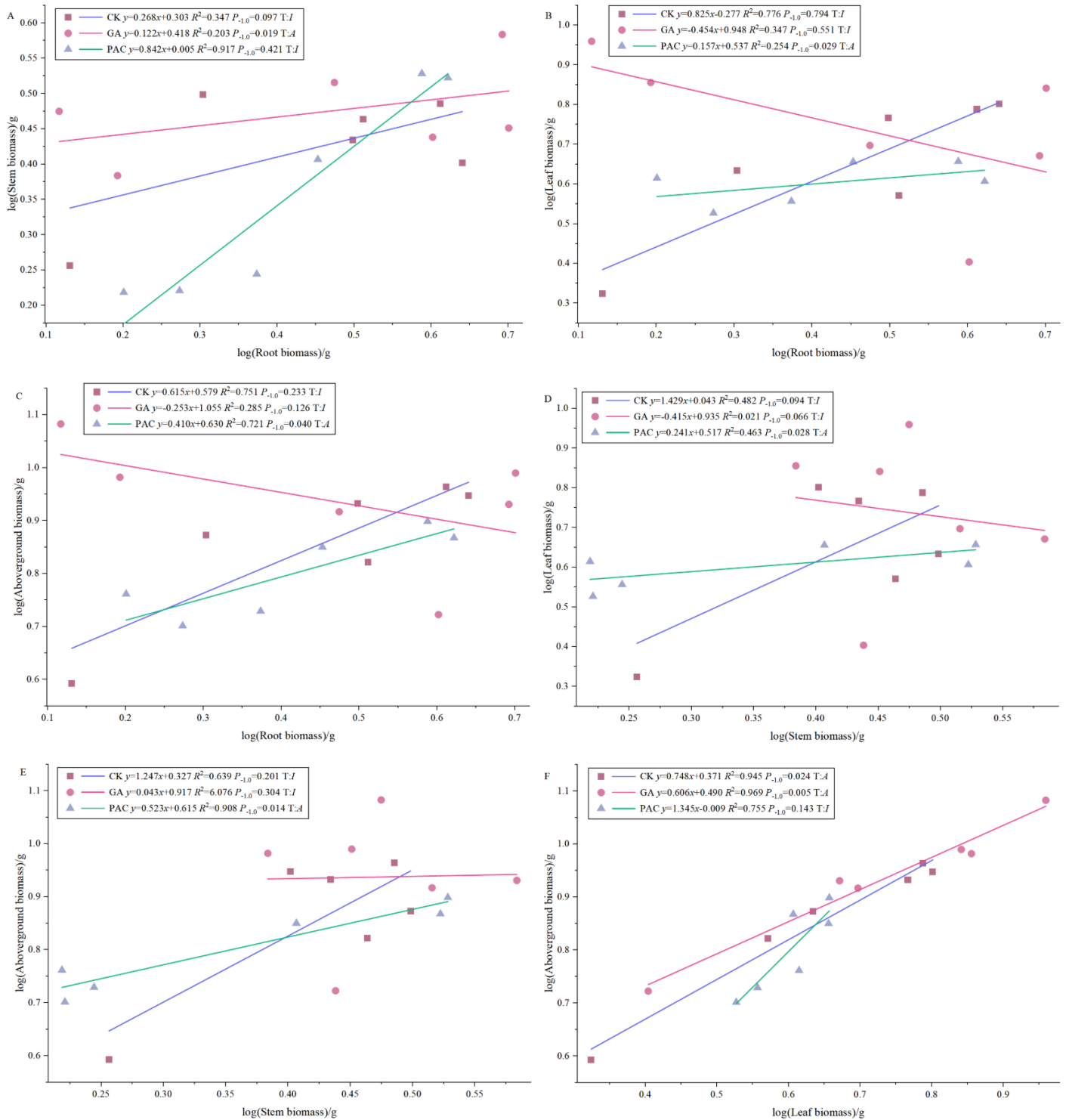


Figure 6

Allometric relationships in September between root biomass and stem biomass (A), root biomass and leaf biomass (B), root biomass and aboveground biomass (C), stem biomass and leaf biomass (D), stem biomass and aboveground biomass (E), and leaf biomass and aboveground biomass (F). The straight lines in the figures represent standardized mean axis (SMA) fitted lines; CK denotes the control treatment, GA denotes gibberellin treatment, and PAC denotes paclobutrazol treatment.

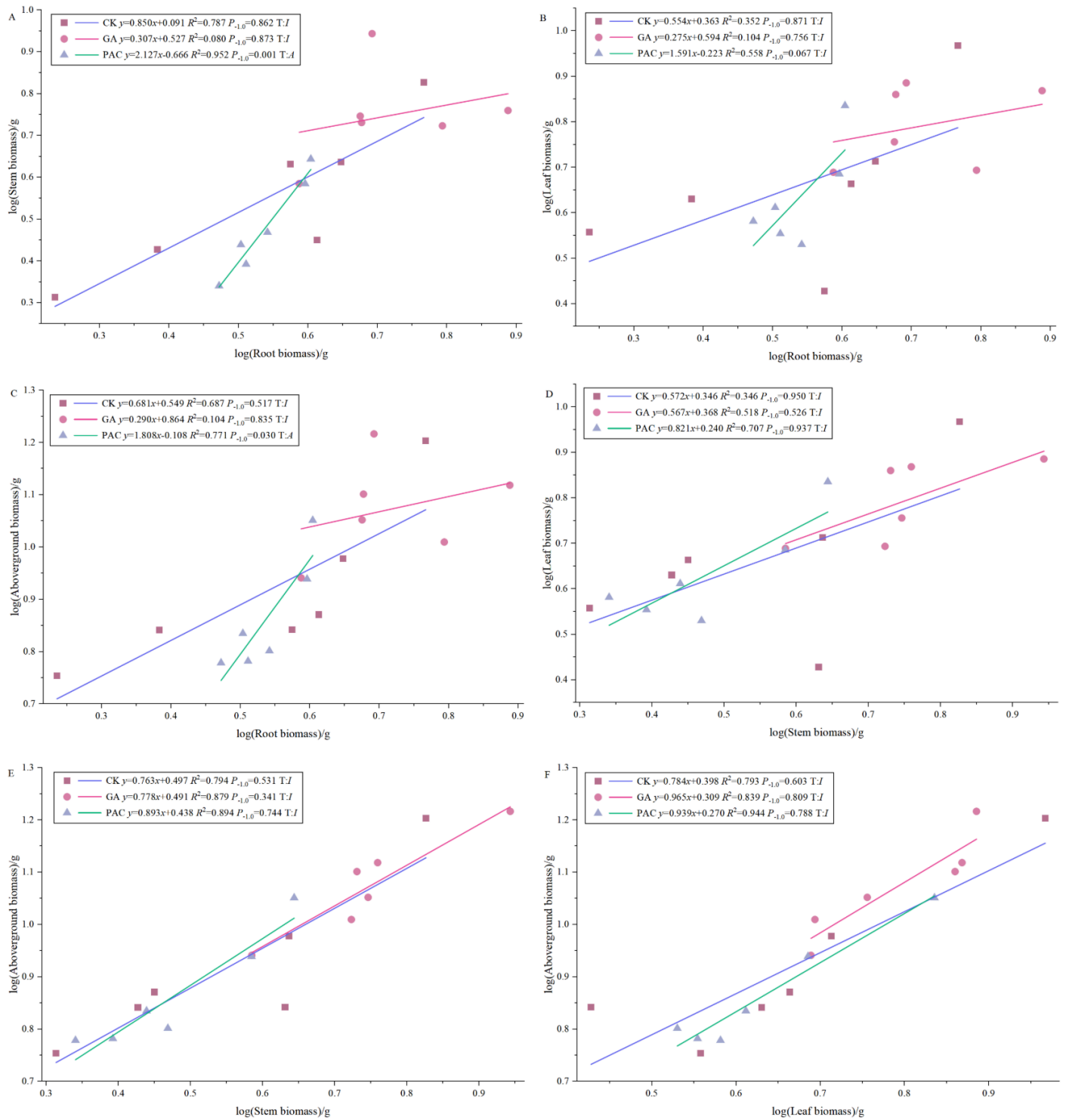


Figure 7

Allometric relationships between root biomass and stem biomass (A), root biomass and leaf biomass (B), root biomass and aboveground biomass (C), stem biomass and leaf biomass (D), stem biomass and aboveground biomass (E), and leaf biomass and aboveground biomass (F) in December. The straight lines in the figures represent standardized mean axis (SMA) fitted lines; CK denotes the control treatment, GA denotes gibberellin treatment, and PAC denotes paclobutrazol treatment.

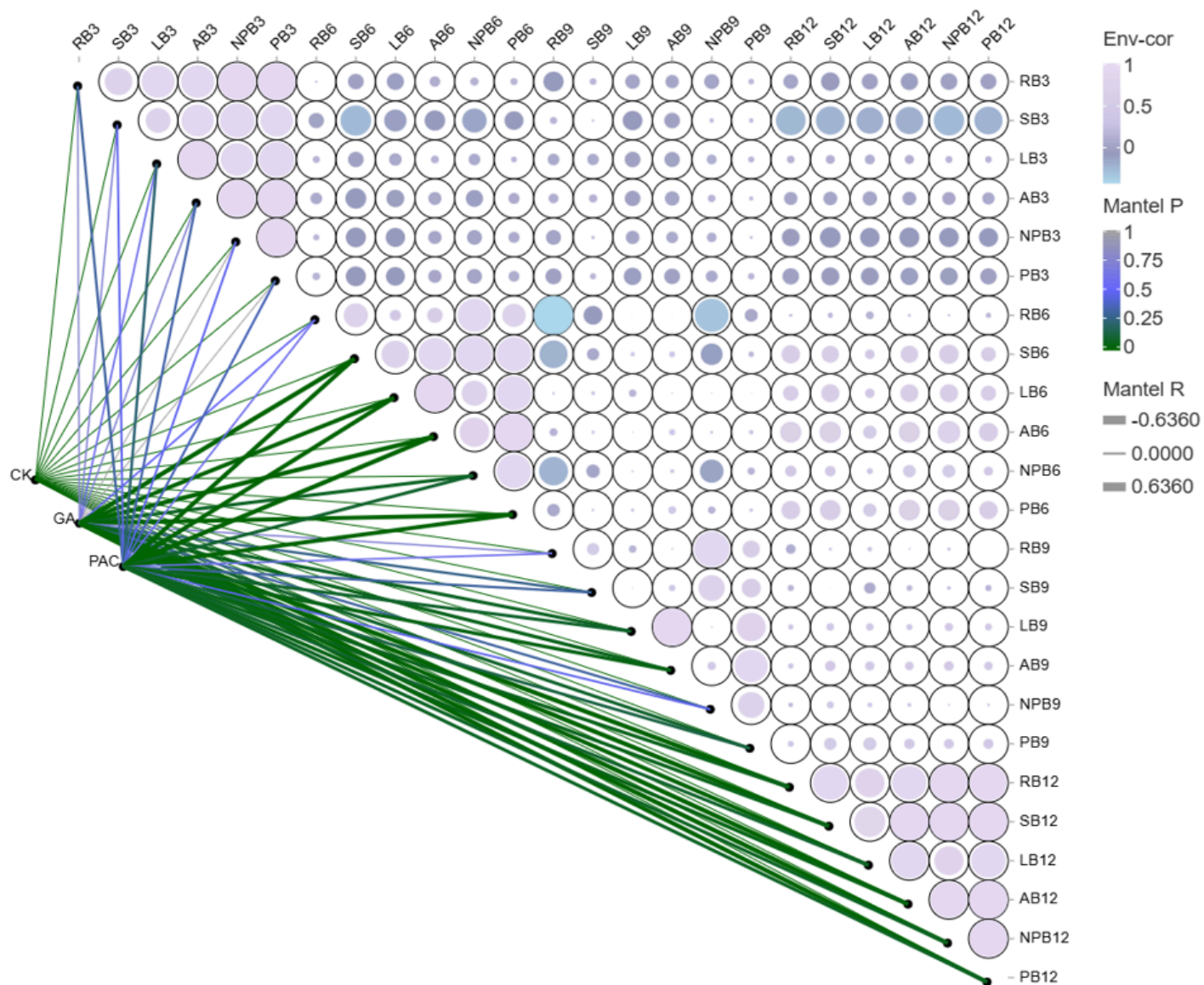


Figure 8

Correlation analysis of biomass traits in *P. yunnanensis* seedlings. The size and shade of the circles in the heatmap indicate the magnitude of the correlation coefficients; the Mantel plot illustrates the strength of the association between exogenous hormone treatment and biomass traits.