defense, adaptation, and stress resistance. When plants are exposed to a certain degree of environmental stimulation, corresponding metabolic regulatory mechanisms may be activated, promoting the synthesis and accumulation of active components such as alkaloids, terpenoids, flavonoids, and phenylpropanoids. Extensive studies have shown that light intensity and quality, temperature, soil moisture, fertility, and salinity can significantly increase or decrease plant secondary metabolite levels, and different types of stress often induce the accumulation of different classes of compounds (Yang et al., 2018; Pant et al., 2021; Qaderi et al., 2023). Therefore, changes in peimine accumulation in *F. thunbergii* can be understood as the result of the combined regulation of primary metabolism, stress signaling, and secondary metabolic pathways by environmental factors.

Under abiotic stress conditions, plants usually activate a series of signal transduction processes, including reactive oxygen species, phytohormones such as jasmonic acid, abscisic acid, and salicylic acid, Ca^{2+} signaling, and mitogen-activated protein kinase (MAPK) cascades. These signals further converge on transcription factors such as MYB, bHLH, AP2/ERF, WRKY, bZIP, and NAC, which coordinately upregulate or downregulate biosynthetic genes in alkaloid, terpenoid, and phenylpropanoid pathways (Kajla et al., 2023; Rabeh et al., 2025). Metabolomics studies have also confirmed that stress-induced changes in primary metabolism, such as alterations in the shikimate pathway, terpenoid backbone pathway, and amino acid metabolism, can further provide precursors, energy, and metabolic flux for the formation of nitrogen-containing alkaloids and other defensive secondary metabolites (Salam et al., 2023). Therefore, moderate environmental stress may promote peimine biosynthesis through a chain reaction involving “signal activation-transcriptional regulation-metabolic pathway redistribution.”

In *F. thunbergii*, existing omics studies have provided direct evidence for this mechanism. The combined treatment of shading and potassium fertilization can significantly increase the contents of peimine, peiminine, imperialine, and other steroidal alkaloids in bulbs. Transcriptomic analysis has identified multiple upregulated genes in the terpenoid/steroidal alkaloid pathway, among which farnesyl pyrophosphate synthase (FtFPS) is regarded as a key hub gene. FtFPS catalyzes the formation of farnesyl pyrophosphate, which is an important precursor for sterol and steroidal alkaloid biosynthesis. Meanwhile, FtFPS can interact with AP2/ERF transcription factors, thereby linking external environmental signals with the activation of the steroidal alkaloid pathway (Liu et al., 2025a). Another fertilization study on *F. thunbergii* showed that organic fertilizer can increase the contents of peimine and peiminine, possibly through the upregulation of ABA signaling and the induction of putative genes related to steroidal alkaloid biosynthesis (Huang et al., 2024a). Therefore, environmental stress has a dual effect on peimine biosynthesis: moderate stimulation can act as an inducing signal to activate secondary metabolic pathways, whereas excessive stress may inhibit growth, reduce photosynthetic carbon supply, and cause metabolic disorder, ultimately leading to unstable accumulation of active constituents.

7.3 Coordination mechanisms between yield formation and peimine accumulation

The goal of *F. thunbergii* production is not only to increase bulb yield, but also to ensure the content of active constituents such as peimine. Therefore, it is necessary to correctly understand the relationship between yield formation and quality formation. Yield mainly depends on photosynthesis, dry matter accumulation, and bulb enlargement, while peimine accumulation is closely associated with secondary metabolic activity. The two processes are both consistent and potentially contradictory. A favorable growth environment can improve plant vigor and bulb yield while providing sufficient substrates for peimine biosynthesis. However, if the environment excessively promotes vegetative growth, dry matter allocation and metabolic direction may shift toward biomass expansion, and active constituent accumulation may not increase synchronously. Studies have shown that shading alone can significantly increase the total active ingredient content in *F. thunbergii* bulbs, but it reduces bulb biomass and yield, showing a typical “high-quality/low-yield” pattern (Liu et al., 2025a).

The coordination between yield and peimine accumulation depends on regulating the growth focus and metabolic allocation of plants at different developmental stages. In the early growth stage, priority should be given to promoting sprouting, leaf expansion, and root establishment, thereby laying the foundation for subsequent material accumulation. During the vegetative growth stage, high photosynthetic efficiency and moderate population growth should be maintained to ensure sufficient assimilate supply. During bulb enlargement and