

quality indicators in Chinese medicinal materials, including *A. macrocephala* (Zhu et al., 2019). Since organic fertilizer can increase atractylone- and lactone-related indices in *A. macrocephala* cultivation, it likely acts on precisely the fraction most relevant to medicinal-grade evaluation (Kim et al., 2016).

Volatile quality formation is mechanistically sensitive to both environment and post-accumulation transformation. For *A. macrocephala*, precipitation during the early growth season had an important effect on volatile-oil accumulation, showing that water and nutrient environment during vegetative and early rhizome development can shape the final volatile profile (Zhu et al., 2019). Environmental analysis also showed that atractylenolide content was robustly associated with soil texture, cation exchange capacity, temperature, and humidity, whereas growth and phytochemical quality were regulated by partly independent environmental networks (Lee et al., 2025). Processing studies add an important quality-evaluation perspective: raw essential oil is rich in atractylon, whereas processing significantly depletes atractylon and increases atractylenolides I, II, and III through time-dependent chemical conversion (Li et al., 2025). Because crude and processed *A. macrocephala* also differ in the number of detected volatile components and in bioactivity profiles, quality evaluation should consider not only total oil yield but also the balance among key volatile markers and their transformation products (Gu et al., 2019).

4.3 Mechanisms of nutrient regulation promoting quality formation of *Atractylodes macrocephala*

The nutrient-regulation mechanism by which organic fertilizer substitution promotes quality formation appears to involve both improved nutrient supply and activation of key biosynthetic enzymes and genes. Studies on medicinal plants consistently show that the biosynthesis of secondary metabolites is sensitive to nutrient status, especially nitrogen and phosphorus, and that fertilization method and application rate must be matched to the target compounds. In *Atractylodes chinensis*, high-phosphorus fertilization promoted the accumulation of volatile-oil components and increased the expression of *ACC* and *FPPS*, while *HMGR* also contributed to sesquiterpene regulation. This is mechanistically relevant to *A. macrocephala* because sesquiterpenes such as atractylone and atractylenolides are key quality constituents, and terpenoid synthesis in *Atractylodes* depends on precursor supply and pathway activity (Sun et al., 2022). Nutrient effects on volatile quality are also seen in other medicinal plants: increasing phosphorus significantly increased essential-oil production in *Vitex negundo*, plausibly because phosphorus supports acetyl-CoA-dependent terpenoid biosynthesis (Peng and Ng, 2022).

Organic substitution adds another layer by reshaping microbial nutrient cycling and root-zone signaling, which can stabilize nutrient release and improve metabolic efficiency. Organic fertilizer increased soil organic matter, total nitrogen, total phosphorus, alkali-hydrolyzable nitrogen, and available phosphorus in rubber rhizosphere, while upregulating microbial genes involved in organic N metabolism, nitrate transport, nitrification, denitrification, and organic P mineralization (Geng et al., 2026). In *Schisandra chinensis*, bio-organic fertilizer altered transcriptomic and metabolomic pathways associated with plant growth and nutrient accumulation, consistent with higher levels of multiple quality compounds (Xu et al., 2025). Nutrient interaction studies further show that N and P coordination can remodel root structure, transporter activity, organic-acid metabolism, and hormone signaling, thereby improving nutrient uptake efficiency rather than simply increasing fertilizer input (Tang et al., 2025). Accordingly, the quality-promoting effect of organic fertilizer substitution in *A. macrocephala* likely arises from a coupled process in which slower but more buffered nutrient release, stronger rhizosphere microbial function, and enhanced terpenoid-biosynthetic signaling together promote the accumulation of lactones, polysaccharides, and volatile oils.

5 Effects of Organic Fertilizer Substitution for Chemical Fertilizers on Stress Resistance and Ecological Benefits of *Atractylodes macrocephala*

5.1 Enhancement of stress resistance in *Atractylodes macrocephala*

Organic fertilizer substitution can enhance the stress resistance of *Atractylodes macrocephala* mainly by improving soil water retention, nutrient buffering, antioxidant capacity, and rhizosphere biological stability. A recent review concluded that organic fertilizers improve tolerance to drought, salinity, heat, and heavy metal stress by improving leaf water status, nutrient homeostasis, chlorophyll synthesis, osmolyte accumulation, antioxidant activity, and stress-related gene expression (Liu et al., 2024). Integrated organic-inorganic nutrition also tends to