

branching and limited development of harvestable organs (Yang and Li, 2017). Similar phenomena have also been observed in leguminous plants, where shading can promote taller and thinner plants while reducing the number of lateral branches and aboveground biomass. For naturally shade-tolerant *T. hemsleyanum*, moderate shading is more likely to result in adaptive elongation and canopy optimization rather than simple etiolation. However, under excessive shading, excessive vine elongation, overly extended internodes, weak stems, and suppressed lateral branching may still occur, ultimately affecting leaf area formation and photosynthetic product accumulation. Therefore, in cultivation, “vine elongation” should not be simply equated with “good growth”; instead, branch number, leaf distribution, vine robustness, and underground tuberous root development should be comprehensively evaluated.

3.2 Effects on leaf morphology and leaf area expansion

Leaves are the main organs through which *T. hemsleyanum* performs photosynthesis and senses changes in the light environment. Therefore, changes in leaf morphology under shading conditions are important manifestations of its low-light adaptation. Leaf traits of *T. hemsleyanum* are sensitive to shading environments and reflect typical shade-leaf characteristics. As shading increases, chlorophyll a, chlorophyll b, and total chlorophyll contents increase, while the chlorophyll a/b ratio decreases, indicating adaptive adjustment of the light-harvesting antenna system to capture limited photons more efficiently under low-light conditions (Dai et al., 2009; Xu et al., 2018). In general, under moderately low-light environments, *T. hemsleyanum* can enhance light capture capacity by expanding individual leaf area, increasing total leaf area, and increasing photosynthetic pigment content. Studies have shown that leaves of *T. hemsleyanum* reach their largest size under approximately 67% shading, whereas full sunlight, 50% shading, and deep shading of approximately 90% all result in smaller leaves (Dai et al., 2009).

Leaf area expansion can increase the plant's absorption range of scattered light, helping compensate for the decrease in light intensity per unit leaf area. These changes are consistent with general patterns observed in shade-tolerant medicinal plants and forest plants, in which moderate shading, compared with no shading or excessive shading, is more conducive to increasing leaf area, improving seedling quality, and enhancing leaf function (Xue et al., 2023; Liu et al., 2026). In other shade-tolerant medicinal plants, low to moderate shading can thin the palisade tissue, increase total leaf thickness, and improve mesophyll structure, thereby promoting light absorption and carbon dioxide diffusion (Li et al., 2025). In *T. hemsleyanum*, increased chlorophyll content under approximately 67%~70% shading, together with improved net photosynthetic rate and other photosynthetic parameters, suggests that its leaf structure and function may also undergo optimization favorable for low-light utilization (Dai et al., 2009; Xu et al., 2018).

However, leaf area expansion does not necessarily indicate increased biomass accumulation. If shading intensity is too high, leaves may show certain shade-adaptive characteristics, such as deeper green color, increased chlorophyll content, or thinner leaf blades. Nevertheless, due to insufficient photosynthetically active radiation, net photosynthetic capacity per unit leaf area may decline, causing leaves to shift from highly efficient production organs to organs with relatively high maintenance costs. Long-term deep shading may also reduce leaf structural stability and stress resistance and increase the risk of disease occurrence. When shading is excessive, the decline in light saturation point and photosynthetic capacity in *T. hemsleyanum* limits carbon acquisition, thereby restricting leaf expansion and total leaf area formation (Xu et al., 2018). Therefore, the effects of shading on leaf morphology should be evaluated comprehensively from three aspects: leaf area expansion, leaf functional maintenance, and photosynthetic efficiency improvement. Among these, moderate shading regimes are more conducive to allowing *T. hemsleyanum* to fully express shade-leaf morphological potential, improve canopy light interception, and promote biomass accumulation.

3.3 Effects on tuberous root enlargement and biomass allocation

The main medicinal organs of *T. hemsleyanum* are enlarged spindle-shaped tuberous roots. These tuberous roots serve both as storage tissues and as pharmacologically active tissues, and their enlargement and dry matter accumulation are directly related to medicinal yield and commercial value (Figure 1) (Ji et al., 2020). The effect of shading environment on tuberous root formation essentially depends on the coordination between aboveground