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REVIEW

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# Potential drivers of fast growth in *Paulownia*

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**Societal Impact Statement**

Trees in the genus *Paulownia* play a crucial role in sustainable forestry, rural economic development, and carbon mitigation due to their rapid growth, exceptional hardwood properties, and prominent carbon sequestration capacity. This review highlights the societal value of *Paulownia* trees and synthesizes several potential drivers of extraordinarily fast growth in these trees. These insights are valuable for maximizing *Paulownia*'s potential for timber production and carbon sequestration, and they also provide a valuable model for studying mechanisms of rapid growth in hardwood trees.

**Summary**

*Paulownia* is a genus of fast-growing deciduous hardwood trees that are economically and ecologically important. Originally from East Asia, *Paulownia* are grown globally for their robust timber, agroforestry, and effective carbon dioxide drawdown, services that arise from their remarkably fast growth. Despite their clear value, the underlying drivers of fast growth in this genus remain poorly understood. Here, we review potential causes of fast growth in *Paulownia* and identify several potential adaptations, including photosynthetic metabolism, non-foliar photosynthesis, tree habit, leaf structure, and hydraulic investment, that may contribute to fast growth in these trees. Our review highlights the paucity of evidence that would enable evaluation of these properties of *Paulownia* species and makes recommendations for future research needed to help explain drivers of fast growth in these important trees. In doing so, this review establishes a promising model system to study rapid growth in hardwood trees, their benefits to plantation cultivation, and potential for bioengineering.

**KEYWORDS**

agroforestry, facultative Crassulacean acid metabolism (CAM), growth rate, hydraulic efficiency, non-foliar photosynthesis, *Paulownia*, resource allocation

## 1 | INTRODUCTION

*Paulownia* (Paulowniaceae) is an economically and ecologically important genus that includes some of the fastest-growing broad-leaved deciduous hardwood tree species in the world (Zhao et al., 2022). The genus *Paulownia* includes between six and thirteen species, the number of which has varied over time with taxonomic reclassifications (Table 1). The *Paulownia* genus has a broad geographic range. Most

**TABLE 1** The taxonomic classifications of *Paulownia* species across time.

| Year | Species | Variation | Reference |
|---|---|---|---|
| 1959 | *P. tomentosa* | | (Hu, 1959) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. kawakamii* | | |
| | *P. elongata* | | |
| | *P. glagrata* | | |
| 1976 | *P. tomentosa* | *P. tomentosa* var. *tsinlingensis* | (Gong, 1976) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. elongata* | | |
| | *P. australis* | | |
| | *P. kawakamii* | | |
| | *P. catalpifolia* | | |
| 1981 | *P. tomentosa* | *P. tomentosa* var. *tsinlingensis* | (Zhu, 1981) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. elongata* | | |
| | *P. australis* | | |
| | *P. taiwaniana* | | |
| | *P. catalpifolia* | | |
| | *P. albiphloea* | *P. albiphloea* var. *chengduensis* | |
| | *P. kawakamii* | | |
| 1990 | *P. tomentosa* | *P. tomentosa* var. *tsinlingensis*<br>*P. tomentosa* var. *lanata*<br>*P. tomentosa* var. *lucida* | (Jiang, 1990) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. elongata* | | |
| | *P. australis* | | |
| | *P. taiwaniana* | | |
| | *P. catalpifolia* | | |
| | *P. albiphloea* | *P. albiphloea* var. *chengduensis* | |
| | *P. lampropylla* | | |
| 1992 | *P. tomentosa* | *P. tomentosa* var. *tsinlingensis*<br>*P. tomentosa* var. *lanata*<br>*P. tomentosa* var. *lucida* | (Xiong & Chen, 1992) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. elongata* | | |
| | *P. australis* | | |
| | *P. taiwaniana* | | |
| | *P. catalpifolia* | | |
| | *P. albiphloea* | *P. albiphloea* var. *chengduensis* | |
| | *P. lampropylla* | | |
| | *P. recurva* | | |
| | *P. jianshiensis* | | |
| | *P. ichangensis* | | |

**TABLE 1** (Continued)

| Year | Species | Variation | Reference |
|---|---|---|---|
| 2000 | *P. tomentosa* | *P. tomentosa* var. *tsinlingensis*<br>*P. tomentosa* var. *lanata*<br>*P. tomentosa* var. *lucida* | (Chen et al., 2000) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. kawakamii* | | |
| | *P. elongata* | | |
| | *P. lamprophylla* | | |
| | *P. ichangensis* | | |
| | *P. jianshiensis* | | |
| | *P. albiphloea* | *P. albiphloea* var. *chengduensis* | |
| | *P. recurva* | | |
| | *P. australis* | | |
| | *P. catalpifolia* | | |
| | *P. henanensis* | | |
| 2013-onward | *P. tomentosa* | *P. tomentosa* var. *tsinlingensis*<br>*P. tomentosa* var. *lanata*<br>*P. tomentosa* var. *lucida* | (F. Li et al., 2013) |
| | *P. fortunei* | | |
| | *P. fargesii* | | |
| | *P. kawakamii* | | |
| | *P. elongata* | | |
| | *P. lamprophylla* | | |
| | *P. ichangensis* | | |
| | *P. jianshiensis* | | |
| | *P. albiphloea* | *P. albiphloea* var. *chengduensis* | |
| | *P. taiwaniana* | | |
| | *P. catalpifolia* | | |

*Paulownia* species have largely remained in their native East Asian range, where they have been cultivated for over 3,000 years (Hu, 1959). However, three species (*Paulownia tomentosa* (Thunb.) Steud., *Paulownia fortunei* (Seem.) Hemsl., and *Paulownia elongata* S. Y. Hu), as well as some interspecific hybrids (e.g., Clone in vitro 112, Shantong, Sundsu11, and Cotevisa 2) have reached global distributions, with *P. tomentosa* being the most broadly distributed species in the genus (Sławińska et al., 2023; Young & Lundgren, 2023).

*Paulownia* trees provide critical and valuable ecosystem services. Their wood has excellent properties, such as lightness, high dimensional stability, and good acoustic resonance, and thus is widely used for making furniture, decorative materials, musical instruments, handicrafts and other products (Rodríguez-Seoane et al., 2020). The genus has attracted widespread attention for use in ecological engineering projects, including ecological restoration and afforestation in areas with difficult terrain, due to its developed root system, barrenness tolerance, adaptability, and heavy metal adsorption by leaves, stems, and roots (Doumett et al., 2008; Rodríguez-Seoane et al., 2020; Wang et al., 2009). *Paulownia* leaves, flowers, fruits, roots, and bark are used as medicine, being specifically effective in curing upper respiratory tract infections, bronchitis, and mumps (Zheng et al., 2009) and, as such, *Paulownia* are considered traditional medicinal plants whose chemical composition, bioactivity, and pharmacological activity are becoming a research hotspot (Škovranová et al., 2024; Xiao et al., 2024; Yang et al., 2024). Thus, *Paulownia* is a lucrative alternative to traditional crops, due to its relatively low resource requirements, high market demand, and significant financial returns (Negruşier et al., 2024).

*Paulownias* are excellent agroforestry trees. They effectively reduce wind damage, increase biodiversity, and enrich soil organic matter (Testa et al., 2022), without significantly shading agricultural fields at times when sunlight is needed most by key crops. For example, *Paulownia* leaves emerge late in the spring and drop early in the autumn, which allows high light penetration through the canopy to maximize intercropping potential with winter wheat (Figure 1). Furthermore, our previous research in the North China Plain found that the average shading effect in *Paulownia* intercropping decreased

**FIGURE 1** ***Paulownia*-wheat intercropping system.** *Paulownia elongata* trees are effectively intercropped with wheat (*Triticum aestivum* Zhengmai 379) at the ground level in Lankao County, Henan Province, China. Photograph taken by Jie Qiao.

exponentially with the total area of the agroforestry systems, which have a consistent tree belt design (i.e., the same tree variety, age, rows, and spacing) (Zhao et al., 2019). Moreover, competition for nutrients and water within the soil is minimized between deep-rooted *Paulownia* trees and shallow-rooted intercrops, giving *Paulownia* a significant advantage compared to most other tree species used in agroforestry (Bojesen Jensen, 2016; F. Li et al., 2008; Zhu et al., 1986). For these reasons, agricultural areas along the broad central and northern plains of China have transformed into exemplary agroforestry zones of *Paulownia* intercropping (Zhu et al., 1986), along with, for example, bamboo (*Phyllostachys heteroclada*) (Chen, 2003), Chinese fir (*Cunninghamia lanceolata*) (Xu et al., 2000), and tea plant (*Camellia sinensis*) (Ni et al., 1990), enabling diversified land use while enhancing the growth of mixed forest components. Furthermore, *Paulownia* plantations sustain relatively abundant understory vegetation, promoting biodiversity across scales.

## 2 | *PAULOWNIA* GROWTH ENVIRONMENT

Optimal growth temperature for *Paulownia* ranges between 24 and 30°C; however, these trees can withstand temperatures down to −20°C and above 40°C (Woods, 2008). Their optimum soil water content is approximately 50% of field capacity (Wang et al., 2020). In regions without artificial irrigation, annual precipitation as low as 500 mm can meet their soil water content needs, although annual rainfall up to 1,000 mm is more suitable (Wang et al., 2020). In fact, *Paulownia* persists in semi-arid Mediterranean regions with low irrigation levels (Testa et al., 2022). *Paulownia* trees, however, are intolerant to flooding and, in stands without effective drainage, prolonged waterlogging or flooding limits growth and can be fatal (Wang et al., 2020). These trees are characterized by a deep rooting system, extensive lateral roots, and a fleshy root cortex, all of which are key adaptations for avoiding water stress. They prefer sandy loam or gravelly soils that are deep and well-aerated, with an ideal soil porosity of over 50% (Woods, 2008). *Paulownia* broadly tolerates soil pH between 5.0 and 8.9, but is more sensitive to soil salinity than most tree species (Chinnusamy et al., 2005; Zeng et al., 2002), with its growth being severely hindered when the total salt concentration of the soil rises above 1 % (Zhu et al., 1986).

*Paulownia* are light-demanding trees with very poor shade tolerance, especially during their sensitive sapling stage when even slight shade can cause deformation (Barbu et al., 2023; Wang et al., 2015). This extreme light sensitivity means that *Paulownia* rarely form uniform forests naturally, and instead usually co-occurs with *Acer*, *Quercus*, and *Juglans mandshurica* hardwood trees to form an upper canopy, or occurs in forest gaps and along forest edges with little shade (Jiang, 1990). In plantations, lateral shading causes crown deviation and narrows the annual rings on the shaded side of the trunk by more than 30% in heavily shaded areas, which significantly reduces wood yield and quality (Jiang, 1990).

## 3 | *PAULOWNIA* HAVE REMARKABLY FAST GROWTH

Compared to conventional hardwood and softwood tree species, *Paulownia* exhibits remarkably fast growth (Ayrilmis & Kaymakci, 2013). *P. tomentosa* particularly stands out, with a biomass production of 50 t/(ha·year), which far surpasses traditionally recognized fast-growing species, such as *Populus* spp., *Salix* spp., *Panicum virgatum*, and *Miscanthus* x *giganteus* 'Nagara' that typically yield between

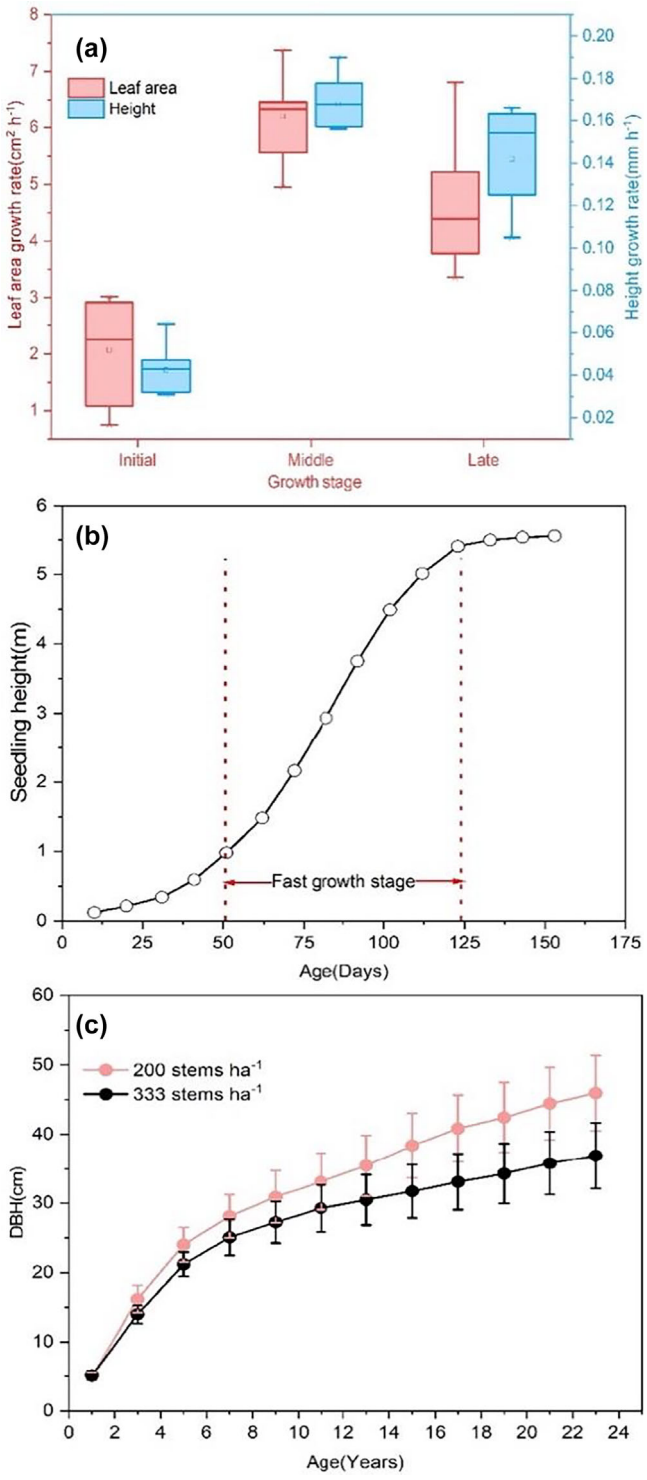


**FIGURE 2** **Growth patterning in *Paulownia*.** (a) Comparison of leaf area (red) and height (blue) growth rates across initial, middle, and late phenological stages of cloned *Paulownia* seedlings. Modified from (Wang et al., 1993). (b) *Paulownia* tree height curves over the first six months. Modified from (Zhou et al., 1996). (c) Growth in diameter at breast height (DBH) in *Paulownia fortunei* 'Yulinensis 1' at two plantation planting densities over 24 years in Liangyuan Forest farm in Shangqiu City, Henan province, China (34°33′18″N and 115°34′44″E). Data show that higher planting density is associated with reduced trunk diameter growth, and this density-dependent growth difference becomes more pronounced with age (*unpublished data*). Error bars are the standard error of the mean.

6 and 17 t/(ha·year) (Domínguez et al., 2017; Marsal et al., 2016). A study on the diurnal growth rhythm across saplings of seven *Paulownia* clones indicated that the leaf area expansion rate can reach over 7 $cm^2$ per hour, while the stem elongation rate reaches up to nearly 0.2 mm per hour (Figure 2a; Wang et al., 1993). Under suitable growth conditions, one-year-old root cutting *Paulownia* trees may attain leaf lengths up to 80 cm (Owfi, 2017), 8 m in height, and up to 12 cm in root collar diameter (RCD) (Zhu et al., 1986). A study of growth patterning in one-year-old saplings found that *Paulownia's* growth (in terms of sapling height) follows a logistic curve, with approximately 80% of the total height increment occurring within a two-and-a-half-month fast-growth stage, as shown in Figure 2b (Zhou et al., 1996). Furthermore, *Paulownia* has strong coppicing ability, such that new growth accumulates at a faster rate after being harvested compared to new sapling growth from seed (Bojesen Jensen, 2016). If *Paulownia* trees are left unharvested, they can attain a life expectancy of up to 80 years, reaching a height of 49.5 m, a diameter at breast height (DBH) of 224 cm, and a wood volume of 34 $m^3$ (Jakubowski, 2022). By forming hollow trunks, *Paulownia* may have developed an adaptive strategy that optimizes mass distribution, increases resistance to gravitational loading, and thus avoids self-buckling even at great heights (Kanahama & Sato, 2023). *Paulownia* can be harvested for purlin or rafter timber after seven growing seasons (Z. Li et al., 2012). If the cultivation objective is plywood or furniture timber, however, the ideal felling age of *Paulownia* is between13 and 20 years, respectively. These young felling times are in stark contrast to most hardwood trees, which take approximately 60 to 80 years to mature and be economically useful (Ayrilmis & Kaymakci, 2013).

## 4 | POTENTIAL DRIVERS OF FAST GROWTH IN *PAULOWNIA*

In the following sections, we propose potential drivers of fast growth in *Paulownia*, linking traits typically associated with fast growth in trees with the available current literature on *Paulownia* and highlighting where more research is needed.

### 4.1 | Specialised photosynthetic metabolism

Photosynthetic capacity is an important factor in plant growth that is primarily driven by photosynthetic metabolism. Plants are generally divided into four main types of photosynthetic carbon metabolism, including $C_3$, $C_4$, $C_2$, and Crassulacean Acid Metabolism (CAM) (Lundgren, 2020; Paulus et al., 2013). Over the past few decades, there have been mixed reports about the type of photosynthesis used by *Paulownia*. Like most trees, *Paulownia* species have traditionally been classified as $C_3$ plants, primarily due to the absence of Kranz anatomy in their leaves (Su et al., 1993). This classification was recently supported by transcriptomics evidence that was consistent with $C_3$ carbon assimilation in the mesophyll (Cao et al., 2021). Despite these lines of evidence, however, many studies have attributed *Paulownia's* fast growth and exceptional carbon sequestration

capacity to $C_4$ photosynthesis (e.g., Ghazzawy et al., 2024; Jakubowski, 2022; Sławińska et al., 2023; Świechowski et al., 2019; Woźniak et al., 2018). $C_4$ photosynthesis is a carbon concentrating mechanism (CCM) that spatially separates $CO_2$ fixation across mesophyll and bundle sheath cell types within the leaf to effectively reduce photorespiration and consequently boost photosynthetic efficiency and ultimately growth under hot and bright environments (Atkinson et al., 2016; Pearcy et al., 1987). The $C_4$ pathway is a highly convergent complex trait that has evolved in ~70 plant lineages independently; however, it is very rarely found in true trees and is not associated with rapid growth rates in the few tree species that do use this CCM (Young et al., 2020).

A recent investigation of photosynthetic phenotypes in *P. tomentosa*, *P. fortunei*, and *Paulownia kawakamii* strongly suggests that these *Paulownia* species do not use $C_4$ photosynthesis (Young & Lundgren, 2023). Indeed, key leaf traits used to define photosynthetic type, such as the $CO_2$ compensation point - the $CO_2$ concentration at which the rate of $CO_2$ uptake through photosynthesis equals the rate of $CO_2$ release through respiration and photorespiration (55.7–63.8 μmol $mol^{-1}$)- and leaf interveinal distance - the average distances between adjacent longitudinal veins (156–225 μm)- were significantly higher in *Paulownia* than values typically measured in $C_4$ plants, while carboxylation efficiency (0.04–0.09 mol $m^{-2}$ $s^{-1}$) and $\delta^{13}C$ stable isotope signatures (−25.59 to −22.22 ‰) in *Paulownia* fell well below values typically measured in $C_4$ plants under similar growth environments (Young & Lundgren, 2023). Furthermore, the same study found very few chloroplasts localized to the bundle sheath tissue of *Paulownia* leaves, suggesting the spatial separation of atmospheric $CO_2$ fixation would be nearly impossible via the dual-cell $C_4$ system used by most $C_4$ plants. These results indicate that *Paulownia* does not employ the $C_4$ CCM.

Unlike $C_4$ photosynthesis, CAM is a CCM that temporally separates $CO_2$ fixation across the day and night, such that CAM plants take in $CO_2$ via open stomatal pores during the night when it is cool and store it in vacuoles until the daytime when it can be mobilized and converted into sugars in the Calvin-Benson-Bassham cycle. In doing so, this pathway effectively saves water, making CAM photosynthesis particularly advantageous in very dry environments. In some plants, CAM is *facultative*, meaning that it can turn on and off depending on the environment, often being induced under water-limited conditions (Cushman & Borland, 2002). Unlike obligate CAM species, which trade off fast growth for exceptional water-saving potential, facultative CAM can facilitate fast growth (Winter & Holtum, 2024).

Two recent studies have suggested that *Paulownia* may fix $CO_2$ via a facultative CAM pathway that supplements $C_3$ metabolism (Cao et al., 2021; Wang et al., 2019). First, Wang et al. (2019) found that genes encoding enzymes used in CAM metabolism for $CO_2$ residue delivery were upregulated in *Paulownia*. Then, Cao et al. (2021) found that the stomata dotted along *Paulownia* leaves remain open through both the day and night, suggesting that active gaseous exchange may be taking place through their stomata at night, which is a common phenotype of CAM plants. Furthermore, they identified differential expression and regulation of photosynthesis genes during the daytime versus the nighttime that were consistent with patterns of carbon assimilation taking place during the night as is typically found in CAM plants. The findings of these two studies are compelling, but not conclusive. Indeed, nocturnal stomatal opening has been observed in several $C_3$ species without association with CAM (Resco De Dios et al., 2019). Furthermore, *Paulownia* leaves are not succulent, which is a morphological prerequisite for vacuolar storage capacity of organic acids in obligate CAM plants, but may not exclude the possibility of facultative CAM in *Paulownia* (Holtum et al., 2016; Sage et al., 2023; Winter & Holtum, 2024). Taken together, patterns are emerging that point to *Paulownia* potentially having evolved a specialized photosynthetic mechanism that remains elusive. Further research is needed to fully elucidate the photosynthetic phenotype of *Paulownia* and determine the extent to which it may contribute to fast growth. For example, 24-hour diurnal gas exchange measurements would confirm or not whether *Paulownia* leaves assimilate $CO_2$ during the night and therefore perform facultative CAM (Cenciareli et al., 2025; Mok et al., 2023). Following this, the degree to which putative facultative CAM then contributes to fast growth with *Paulownia* would require additional experimental validation. In addition, the benefits of respiration for rapid growth should be considered, as it functions as a process complementary to, rather than opposing, photosynthesis (Amthor, 2025).

## 4.2 | Non-foliar photosynthesis in saplings

While photosynthesis is typically associated with leaves, it can also occur in any chlorophyll-rich tissues throughout a plant, such as green stems, bracts, petals, pods, and seeds, to effectively boost whole plant carbon assimilation (Aschan & Pfanz, 2003; Simkin et al., 2020). One distinctive feature of non-foliar photosynthesis is its dual origin of $CO_2$. First, internal leaf $CO_2$ can originate from atmospheric $CO_2$ that has diffused from the atmosphere into the cells through stomatal pores, where it can be fixed by ribulose-1,5-bisphosphate carboxylase (Rubisco) in leaf tissue via the Calvin–Benson–Bassham (CBB) cycle. Additionally, $CO_2$ can also be released from respiration or photorespiration into the leaf, which can then be refixed via the CBB cycle (Millar et al., 2011; Simkin et al., 2020).

The relative contributions of non-foliar photosynthesis to whole plant photosynthetic carbon assimilation remain contentious and appear to be strongly species-dependent (Lawson & Milliken, 2023). Photosynthesis in cucumber (*Cucumis sativus*) fruits, for example, provides nearly one tenth of the whole plant carbon assimilation and nearly 90 % $CO_2$ released by respiration is refixed in these fruits (Sui et al., 2017). Indeed, non-foliar photosynthetic tissue may be particularly important for refixing respired $CO_2$, which is likely to become critical when the diffusion and supply of external $CO_2$ are limited (Lawson & Milliken, 2023). Foliar and non-foliar photosynthesis may have distinct photosynthetic characteristics. For example, photosynthetic efficiency within the rind of Satsuma Mandarins (*Citrus unshiu*) is approximately fivefold higher than that of its leaves under a low


**FIGURE 3** **Photosynthetic stems in *Paulownia* saplings.** Photographs showing (a) green stems; (b) lenticels along the main stem; and (c) lenticels and vertical cracks in maturing trees. Photographs taken by Jie Qiao, Baoping Wang, and Chaowei Yang, respectively.

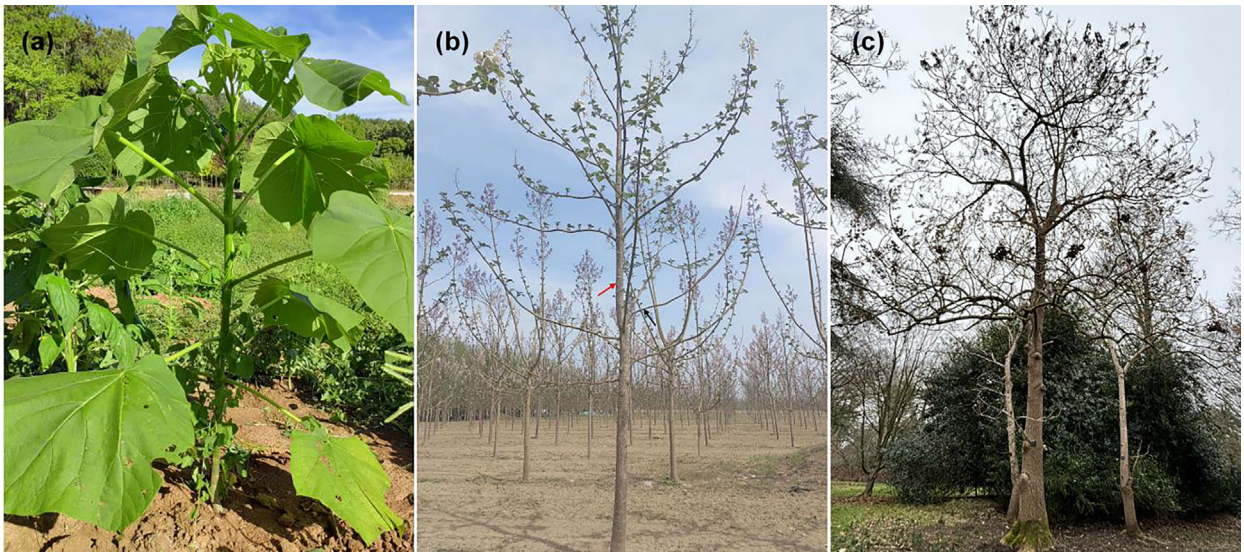


**FIGURE 4** **Monoaxial growth and pseudo-dichotomous branching in *Paulownia* saplings and mature trees.** Photographs showing (a) monoaxial growth in saplings and (b) the terminal bud dies in winter, and the lateral bud near the top forms a pair of lateral branches, and the growth of the stem exhibits pseudo-dichotomous branching. One of the two pseudo-dichotomous branches is often stronger (red arrow) than the other (black arrow). In *Paulownia fortunei*, the former grows upwards in the direction of the main stem and thus contributes to the extension of the stem, while the latter gradually dies back due to light/nitrogen/water competition. Panel (c) shows two balanced branches in *Paulownia tomentosa*, which limits the extension of the main stem. Photographs taken by Yang Zhao.

light intensity of 13.5 mol $m^{-2}$ $s^{-1}$ (Hiratsuka et al., 2015). Indeed, photosynthesis in green non-foliar tissues is widely accepted to have a similar photosynthetic pathway to that of mesophyll (Henry et al., 2020; Hiratsuka et al., 2015; Trainin et al., 2022). However, foliar and non-foliar tissues have also been documented to use different photosynthetic pathways. In the $C_3$ crop tobacco, for instance, cells surrounding the xylem and phloem within the stems and petioles exhibit biochemical and anatomical characteristics of $C_4$ photosynthesis (Hibberd & Quick, 2002).

In trees, photosynthesis in green, non- or low-lignified trunk and stem tissue can contribute significantly to carbon fixation and stem growth, while also improving hydraulic function and drought survival (Ávila-Lovera et al., 2024; Chen et al., 2021; Kocurek et al., 2020; Sun et al., 2021). Previous studies indicate that stem photosynthesis in desert shrubs operates between 16 and 60% of leaf photosynthetic rates (Ávila et al., 2014), and this strong stem photosynthetic capacity is largely maintained throughout the dry season (Ávila-Lovera et al., 2017), and can reach more than 70% of leaf photosynthetic rates in the arid-adapted wild cherry (*Prunus arabica*) (Brukental et al., 2021). In addition to the main trunk/stems of saplings and green-barked trees, current-year branches can also effectively contribute to whole plant net carbon assimilation (Berveiller et al., 2007). Studies have quantified the importance of stem photosynthesis in trees, finding that it contributes approximately 11% to branch tissue growth in *Eucalyptus miniata* (Cernusak & Hutley, 2011), 24% to stem growth in *Populus nigra* (Bloemen et al., 2013), and up to 56% to trunk diameter in *Arctostaphylos manzanita* (Saveyn et al., 2010).

In non-succulent plants, stem photosynthesis can be divided into two types: direct stem net photosynthesis and indirect stem $CO_2$ recycling photosynthesis (Ávila et al., 2014). Direct stem net photosynthesis is characterized by the presence of stomata or lenticels along the stem epidermis, which allow an entry point for atmospheric $CO_2$ into the photosynthetic cells of green tree trunks, stems, and branches (Cernusak & Cheesman, 2015). Here, chlorophyll-rich trunks/stems/branches engage in active $CO_2$ assimilation via the CBB cycle to increase whole plant carbon assimilation and water-use efficiency. By contrast, the more common indirect stem $CO_2$ recycling photosynthesis occurs in shrub and tree species with smooth bark surfaces, which effectively trap respired $CO_2$ and allow for higher light penetration, and involves the refixation of $CO_2$ produced by underlying respiratory processes or from released $CO_2$ transported during transpiration. This indirect stem recycling photosynthesis reduces carbon respiratory losses to boost whole plant net carbon assimilation (Berveiller et al., 2007; Cernusak & Cheesman, 2015; De Roo et al., 2020).

While *Paulownia* may engage one or both types of this non-foliar photosynthesis in their trunk/stems/branches throughout their life, it may be particularly important during the sapling stage for these trees. Unlike most trees, *Paulownia* stems remain green and non-lignified throughout the first year of growth (Figure 3a), with numerous lenticels developing along the stem during this year-long sapling stage. As *Paulownia* trees mature in their second year of growth, their epidermis gradually transitions from green to grey-brown or black (Figure 3b), stem lignification increases, and lenticels transform into vertical cracks (Figure 3c) along the bark surface (Jakubowski, 2022). These traits suggest that active stem net photosynthesis occurs along the main trunk of *Paulownia* during their first year of growth, which would give an initial boost to the whole-plant carbon acquisition, allowing these trees to grow tall quickly. While stem photosynthesis has been characterized in other fast-growing trees, including *Eucalyptus urophylla* (Chen et al., 2021), *Poplar tremula* (De Roo et al., 2020), and *Salix matsudana* (Liu et al., 2019), it remains uncharacterized in *Paulownia*. Understanding whether *Paulownia* effectively performs direct stem net and/or indirect recycling photosynthesis and their implications for growth requires further investigation.

Further research is needed to address these questions around the potential contribution of non-foliar photosynthesis to rapid growth in *Paulownia* trees. For example, one simple approach to start to answer these questions would be to characterize the presence or absence of stomata along the non-foliar green surfaces. If stomata are indeed present, then gas exchange measurements could confirm or not $CO_2$ flux in these non-foliar tissues. Furthermore, long-term light-exclusion experiments, for example by covering stems in aluminum foil (Valverdi et al., 2023) or performing leaf defoliation (Natale et al., 2023), would directly quantify the contribution of stem photosynthesis to seedling growth. Finally, patterns of carbon- and oxygen-isotope discrimination may shed light on the fraction of woody biomass produced by net stem photosynthesis and refixation (Cernusak & Hutley, 2011).

### 4.3 | Growth habit

The monoaxial growth strategy, which is characterized by a single, strictly unbranched stem, is associated with rapid height growth in trees (Kohyama, 1987). Monoaxial trees typically adjust the petiole length of leaves within the crown to reduce self-shading (Aoyagi et al., 2024). Together, the monoaxial growth strategy allows trees to grow vertically at a fast rate and with cheap extension costs, so that they can rapidly take advantage of canopy gaps and minimize competition (Aiba & Nakashizuka, 2007). *Paulownia* saplings are monoaxial, exhibiting the specialized leafing pattern, with their petiole length decreasing from the top to the bottom of the stem (Figure 4a). As *Paulownia* trees age, however, they gradually transition to a pseudo-dichotomous branching pattern (Zhao et al., 2021), whereby the terminal axis stops growing and growth only continues via lateral branches (Figure 4c). Similar to petiole length in young *Paulownia* saplings, branch lengths that form in older saplings also increase from the top to the base, as do the angles between branches and stems (Figure 4b,c). The shift from monoaxial to pseudo-dichotomous growth habit after the first year of growth suggests that *Paulownia* prioritizes rapid and inexpensive height growth during its first year of life to quickly outcompete and escape its neighbors. Further study is required to determine how the crown architecture of this growth habit, including total leaf area, the distribution of leaf and branch angles, and the resulting patterns of canopy light transmission, interception, and light use efficiency (Aoyagi et al., 2024; De Mattos

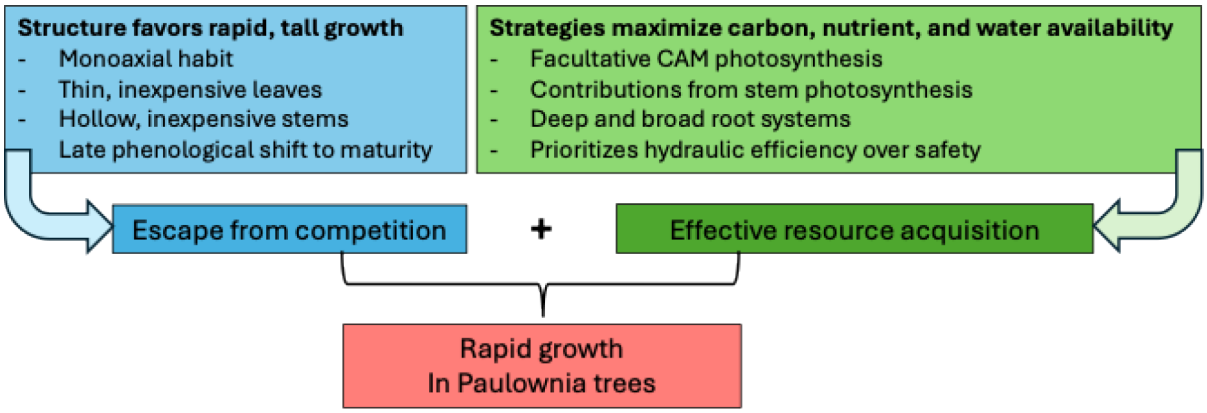


**FIGURE 5** **Conceptual diagram collating the topics discussed in this review.** *Paulownia* present several traits that facilitate their escape from competition via specific habit, structure, and phenological strategies (blue). Potential use of specialist photosynthetic metabolism and non-foliar photosynthesis would maximize carbon-use efficiency, whilst a deep root system and large vascular structures could enhance nutrient and water acquisition (green). Together, strategies that effectively evade competition coupled to effective resource acquisition appear to underpin fast growth in paulownia trees. However, structured, hypothesis-driven experiments are needed to validate these proposed drivers of fast growth in *Paulownia*.

et al., 2020) at both sapling and mature stages, efficiently contributes to overall tree growth.

## 4.4 | Leaf structure

The leaf structure of *Paulownia* may contribute to its high photosynthetic capacity and rapid growth. For example, *P. elongata* exhibits a high stomatal density of 630.06 $mm^{-2}$ (Fan et al., 2006), well above those values reported for several *Populus* species (Sakoda et al., 2020; Wang et al., 2024), another well-known rapid-growth tree species. Because stomatal density is positively correlated with $CO_2$ exchange, net photosynthesis, and biomass production (Sakoda et al., 2020; Tanaka et al., 2013), having high stomatal density could provide an anatomical advantage to growth. In addition, mesophyll architecture can be tuned to raise mesophyll conductance by expanding the surface area of mesophyll cells exposed to the intercellular airspace (Baillie & Fleming, 2020; Lehmeier et al., 2017). *Paulownia* leaves have been shown to possess unusually large mesophyll air spaces (Jiang, 1990), which could enhance internal $CO_2$ diffusion and, consequently, photosynthetic performance.

Specific leaf area (SLA), or the light-capturing surface area per unit dry mass investment, is an important factor in photosynthetic-nitrogen relations (Milla & Reich, 2007; Reich et al., 1998). Indeed, *Paulownia* saplings have remarkably large, thin leaves that can exceed one meter in length and have high SLA (Zhu et al., 1986), like many monoaxial trees, which typically have large leaves with low construction costs (Aiba & Nakashizuka, 2007). Leaves with high SLA increase light interception in saplings and younger trees (Augspurger & Bartlett, 2003), and greater light interception has been linked to greater water and resource allocation leading to improved photosynthesis, growth rates and, ultimately, woody mass production (De Mattos et al., 2020; Pongpattananurak et al., 2025; Ruiz-Robleto & Villar, 2005; Steppe et al., 2011). After the first year of growth, however, *Paulownia* leaves transition to become smaller and thicker (lower SLA) (Icka et al., 2016), which may indicate an evolutionary adaptation to cope with greater water limitation in mature trees (Aparecido et al., 2017; England & Attiwill, 2006).

Leaf structural costs are influenced by multiple leaf traits in addition to SLA. For example, trade-offs between photosynthesis and respiration and between structural and non-structural carbon accumulations, and plant nutrient characteristics (i.e., plant elemental stoichiometry, such as N allocation trade-off). Despite their recognized importance for plant performance, these interacting determinants of construction cost have yet to be examined in *Paulownia*. Therefore, dedicated studies are still needed to clarify how each factor shapes the leaf economic strategy of this genus.

## 4.5 | Reduced investment in hydraulic safety

As discussed above, *Paulownia* is renowned as tall, fast-growing trees. In one remarkable example, a *P. fortunei* tree in Sichuan Province, China, grew to 21.7 m high and with a volume of 6.65 $m^3$ over just 18 years (Zhu et al., 1986). This significant vertical growth rate requires the production of additional xylem conduits to maintain vascular continuity from where water is absorbed in the roots to where it is transpired from the crown foliage. Some have hypothesized that this vascular connectivity can create a context-dependent trade-off between hydraulic efficiency (i.e., water transport capacity) and safety (i.e., resistance to embolism) (Hacke et al., 2006; Prendin et al., 2018; Sperry, 2003). In support of this theory, Van Der Sande et al. (2019) found that enhanced hydraulic *safety* was associated with higher wood density, greater leaf dry mass content, lower stomatal conductance, and lower photosynthetic efficiency across a study of 18 tree species, which suggests that high-cost dense wood and leaves with

lower photosynthetic activity play key roles in enhancing hydraulic safety in trees (van der Sande et al., 2019). In further support, Santiago et al. (2004) found that greater hydraulic *efficiency* was associated with higher rates of gas exchange in the leaves of 20 canopy-forming trees, facilitating an acquisitive life history strategy of fast resource acquisition and growth. Therefore, one could conclude that *Paulownia* may prioritize hydraulic efficiency over safety. Indeed, *Paulownia* trees have low wood density ranging from 220 to 350 kg $m^{-3}$ (Jakubowski, 2022); compared to a typical range of 300–600 kg $m^{-3}$ across most tree species (Saranpää, 2003) which is linked to greater hydraulic efficiency and rapid height growth (Aiba & Nakashizuka, 2007; Van Der Sande et al., 2019). However, trade-offs between hydraulic safety and efficiency are not inevitable (Maherali et al., 2004), and some tree species can evolve phenotypes that balance both safety and efficiency (Gleason et al., 2016; Liu et al., 2021). If trade-offs between hydraulic safety and efficiency exist, then natural selection should favor high efficiency in wet environments and high safety in arid environments (Sperry et al., 2008). A 7-year multisite clonal test at three sites spanning the temperate to subtropical regions of China indicated that *Paulownia* typically grows best in wet environments with a mean annual precipitation of 1,690 mm (Zhao et al., 2022), Furthermore, one site in Hubei province experienced a severe meteorological drought in 2022—the worst in 60 years—which led to dieback in *Paulownia* branch tips while neighboring slower-growing Chinese fir plantation trees appeared unaffected throughout the drought period (*personal observation*). These examples lend support to the idea that *Paulownia* prioritizes hydraulic efficiency over safety. However, the details behind the hydraulic strategy of *Paulownia* and its role in rapid growth remain unclear. Future studies should therefore investigate how biomass allocation, leaf water relations, stem xylem anatomy and function, and the coordination of these traits (Medeiros et al., 2016) function together to shape overall hydraulic performance.

## 5 | CONCLUSION

*Paulownia* are remarkable hardwood deciduous trees with significant economic and ecological value that have among the fastest recorded growth rates in the plant kingdom. Despite their societal value, the drivers of fast growth in these trees remain unknown. Here we propose several possible underlying facilitators of fast growth in the genus, including potential use of facultative CAM photosynthetic metabolism, non-foliar sapling stem photosynthesis, a sapling monoaxial growth habit, inexpensive structural costs, and prioritized hydraulic efficiency, which may all function together to convey extraordinarily fast growth in these trees (Figure 5). Furthermore, we conclude that *Paulownia* trees prioritize rapid growth via a combination of these factors, specifically during the first 12 months of growth, to effectively outcompete or escape their neighbors. Comprehensive investigations are required to gain a more holistic understanding of the mechanisms behind the rapid growth of *Paulownia*. Elucidating these drivers could yield a physiological model system of the rapid growth in hardwood tree species and provide pivotal insights that would be broadly applicable to sustainable plantation management, conservation, bioenergy production systems, and plant biotechnology.

## AUTHOR CONTRIBUTIONS

MRL and YZ conceived and wrote the manuscript.

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## CONFLICT OF INTEREST STATEMENT

No conflict of interest declared.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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