Received: 2 June 2022 | Revised: 9 October 2022 | Accepted: 26 October 2022

DOI: 10.1002/ppp3.10343

RESEARCH ARTICLE

Plants People Planet PPF Open Access

C_4 photosynthesis in *Paulownia*? A case of inaccurate citations

Sophie N. R. Young | **Marjorie R. Lundgren**

Lancaster Environment Centre, Lancaster University, Lancaster, UK

Correspondence
Marjorie R. Lundgren, Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, United Kingdom.
Email: m.lundgren@lancaster.ac.uk

Funding information
Natural Environment Research Council, Grant/Award Numbers: NE/S007423/1, T043970, S007423; UK Research and Innovation, Grant/Award Number: MR/T043970/1

Societal Impact Statement

C_4 photosynthesis is an ultra-efficient mode of photosynthesis found in some of our most productive crop species yet is notably rare in trees. Given C_4 photosynthesis is associated with high yield in herbaceous species, especially under hot and dry conditions, C_4 trees may seem an attractive prospect for biomass production and carbon sequestration in a rapidly changing climate. This may explain why some in the literature have optimistically linked C_4 photosynthesis with the exceptionally fast-growing tree Paulownia. However, this claim is lacking in evidence and represents an example of poor citation practices leading to the spread of misinformation.

Summary

- The rapid growth of trees in genus *Paulownia* (Paulowniaceae) has been attributed in the literature to their use of C_4 photosynthesis, a complex trait that confers increased photosynthetic efficiency under certain environmental conditions. After careful examination of citations used to support the idea that *Paulownia* species use C_4 photosynthesis, we find that there is no data underpinning this claim. Despite this, many investment schemes utilise information about the physiology of *Paulownia*, including photosynthetic type, to legitimise the use of Paulownia trees for financial investment and carbon offsetting.
- This study uses leaf physiology, anatomy and stable isotope data to determine whether or not three species in *Paulownia* (*Paulownia tomentosa*, *Paulownia fortunei* and *Paulownia kawakamii*) use C_4 photosynthesis. These data are compared with existing data for C_3 and C_4 woody species in the literature.
- We show that the leaf physiology, anatomy and stable isotope phenotypes of the three Paulownia trees considered in the study are not consistent with those of C_4 plants.
- Our findings highlight how inaccurate citation of scientific findings can contribute to the spread of misinformation beyond the scientific community, as some of those promoting investments in Paulownia plantations reference the photosynthetic superiority of *Paulownia* as a means to legitimise its use in carbon offsetting.

KEYWORDS

C_4 photosynthesis, carbon offsetting (schemes), inaccurate citations, *Paulownia*, research integrity, trees

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1 | INTRODUCTION

Trees in genus *Paulownia* (Paulowniaceae) have great cultural significance in East Asia, where they have long been recognised for their potential as ornamental, medicinal and timber species (Hu, 1961; Li, 1578; Nagata et al., 2013; Zhu et al., 1986). *Paulownia* contains eight tree species, which form a monophyletic group (Li et al., 2020), hereafter referred to collectively as *Paulownia*. Paulownia trees are native to East Asia, where they are particularly widespread in South Korea, China and Japan (Hu, 1961, Figure 1. They have been introduced to many other areas globally, including the United States and Europe in the mid-19th century (Breck, 1851; Browne, 1846; Meehan, 1853). The accounts by Browne (1846), Breck (1851) and Meehan (1853) all remark on the desirable ornamental properties and fast-growing nature of specimens of Paulownia, which were being readily propagated by root cuttings (Hu, 1961), suggesting that the introduction of these trees to the United States and Europe was deliberate or at least that the trees were deliberately retained following an accidental introduction. One (unsubstantiated) theory in the literature as to how an accidental introduction could have occurred is the use of the feathery seeds of Paulownia as packing material by Chinese porcelain exporters, resulting in the dispersal of Paulownia along trade routes (Del Tredici, 2010; Yadav et al., 2013). The small, winged seeds of Paulownia are readily dispersed by wind and produced in their thousands by each fruit, with a single tree producing as many as 20 million seeds in 1 year (Carpenter et al., 1983; Carpenter & Smith, 1979; Nagata et al., 2013). The prolific seed production and aforementioned fast-growing nature of Paulownia favour its invasive spread (Williams & Wang, 2021), and indeed, *Paulownia tomentosa* in particular has been recognised as invasive in both the United States

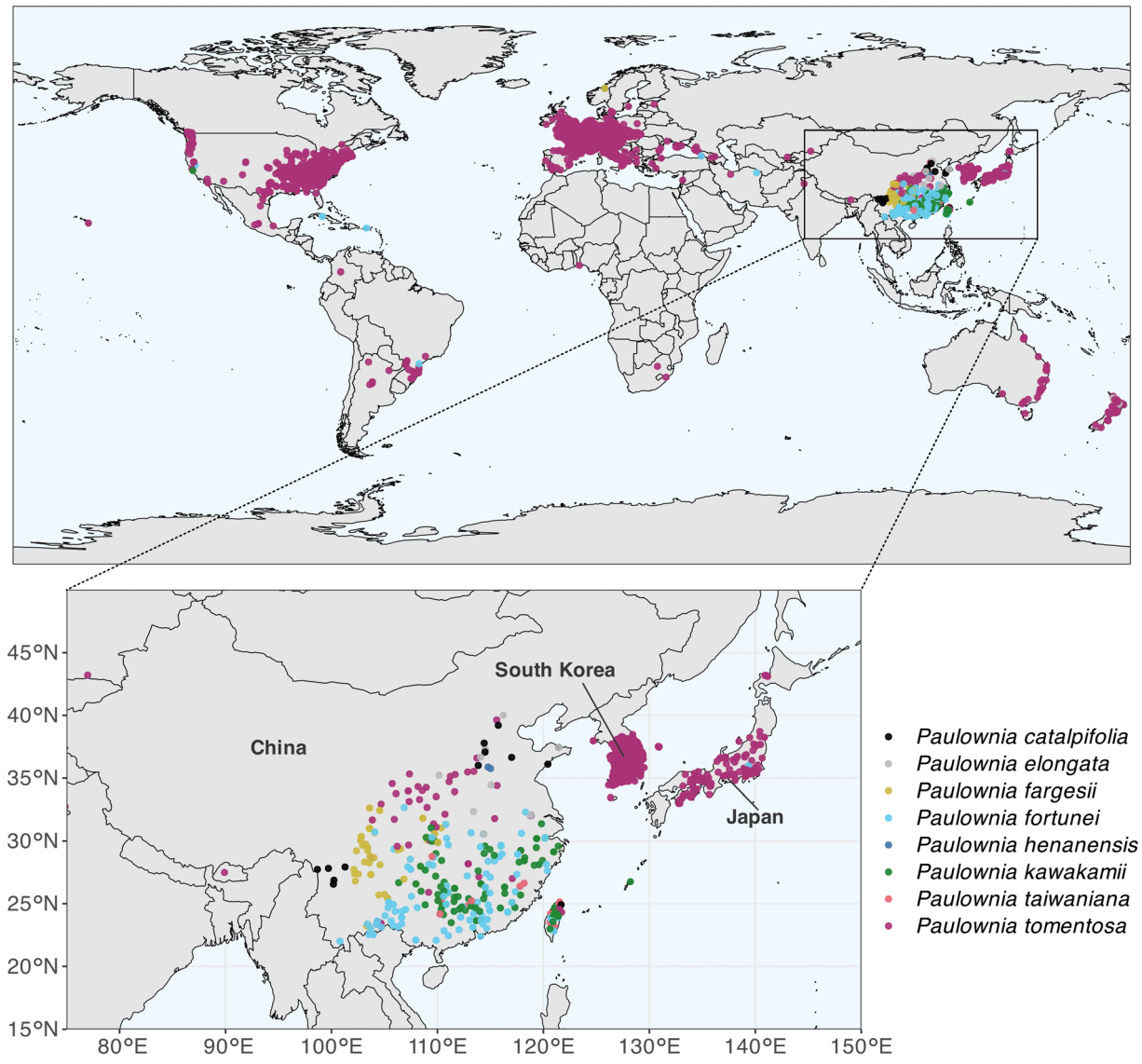


FIGURE 1 Map of the global distribution of the eight species in *Paulownia*. Occurrence data for the eight species in *Paulownia* were obtained from the Global Biodiversity Information Facility (GBIF). Their native range of Southeast Asia is expanded to show this centre of diversity, in which all eight species are found.

and Europe (CABI, 2022; Essl, 2007; Langdon & Johnson, 1994; Texas Invasive Species Institute, 2022). As such, Paulownia trees are both ecologically relevant and economically important species.

Timber produced by Paulownia trees is lightweight and strong with many desirable properties such as resistance to decay, moisture and fire (El-Showk & El-Showk, 2003; Hu, 1961; Li et al., 2020). As such, this timber has historically been used as a building material, as well as for making furniture and musical instruments (Hu, 1961; Zhu et al., 1986). The use of Paulownia wood for furniture in Japan has given rise to the custom of commemorating the birth of a daughter with the planting of a Paulownia tree. This tree is then harvested on the occasion of the daughter's marriage and used to build a wedding chest for the marital home (Nagata et al., 2013). This custom illustrates not only the cultural significance of Paulownia in Japan but also the fast-growing nature of Paulownia trees, given that a single tree is sufficient to prepare a large item of furniture after less than 20 years of growth. Indeed, well-managed Paulownia trees can be harvested for timber after just 5 years, after which time they have been observed to reach an average of 7.9–11.1 m in height (depending on species) with trunks measuring an average of 12.9–18.0 cm in diameter at breast height when grown in Northern China (Zhu et al., 1986). Some Paulownia trees may be able to grow even faster than this: a 5-year-old tree was observed to have reached 17 m in height (Yoon & Toomey, 1986), and a single tree propagated from root cuttings in Szechuan Province in 1977 reportedly attained 10.38 m in height after just one growing season (Zhu et al., 1986).

In the last 50 years, several new potential applications have been identified for these fast-growing Paulownia trees in addition to their longstanding use as ornamental and timber species. In particular, Paulownia has been proposed for use in phytoremediation, as a biomass crop, as a source of green manure, as an agroforestry species and as an investment for carbon-offsetting (Zhu et al., 1987; Woods, 2008; Woźniak et al., 2018; Magar et al., 2018; Zhang et al., 2020; Costea et al., 2021; Testa et al., 2022, World Tree [www.worldtree.eco], Carbon Plantations [www.abundanceinvestment.com/invest-now/carbon-plantations]). Many of the studies and organisations that propose these uses for Paulownia attribute the rapid growth of these trees to their use of the exceptionally efficient C_4 type of photosynthesis. This claim has persisted in the literature for more than 10 years but appears to arise from inaccurate citation practices rather than empirical data (Table 1).

The idea that C_4 photosynthesis is responsible for the rapid growth of Paulownia trees is unlikely given that C_4 photosynthesis is not associated with rapid growth in trees. It is true that the physiology of C_4 plants mean that they have higher overall photosynthetic efficiency, and by extension plant yield, than C_3 plants under certain conditions, including in hot, dry and saline environments (Long, 1999). Furthermore, C_4 photosynthesis has indeed been associated with

TABLE 1 Examples of papers and reports that claim Paulownia trees use C_4 photosynthesis

Citation	Source type	Quote (and citation[a] if present)	Problem with citation
Jakubowski (2022)	Research article	"Paulownias perform photosynthesis based on C4-cycle enzymes (Woods, 2008), as opposed to the classical C3-cycle characteristic of most plants (Sage & Sultmanis, 2016)."	The report by Woods which is cited here does state that Paulownia is C_4 but lacks any evidence to support this claim. The Sage and Sultmanis review cited discusses possible reasons for the global lack of C_4 forest-forming trees.
Dżugan et al. (2021)	Research article	"Paulownias—the C4-photosynthesis plants—belong to the fastest growing trees in the world (Ayan et al., 2006; Woods, 2008)."	The study by Ayan et al. investigates the growth of Paulownia seedlings with no reference to their photosynthetic type. The report by Woods which is cited here does state that Paulownia is C_4 but lacks any evidence to support this claim.
Costea et al. (2021)	Research article	"Paulownia is a C_4 photosynthetic type woody tree …"	Costea et al. offer no citation and insufficient evidence to support this statement.
Swiechowski et al. (2019)	Research article	"*Paulownia* sp. genus developed the C4 photosynthesis (Icka et al., 2016)."	The paper by Icka et al. which is cited here does state that Paulownia is C_4 but lacks any evidence to support this claim.
Woźniak et al. (2018)	Research article	"The *Paulownia* spp. is one of the few species of tree that is characterised by the presence of a C4 photosynthesis pathway."	Woźniak et al. offer no citation or evidence to support this statement.
Icka et al. (2016)	Research article	"Paulownia produces C_4 type photosynthesis with a high level of organic matter in their leaves (Woods, 2008)."	The report by Woods which is cited here does state that Paulownia is C_4 but lacks any evidence to support this claim.
Woods (2008)	Report	"Paulownia is a tree with the C_4 photosynthetic pathway that increases the rate of leaf sugar production in warm conditions."	Woods offers no citation or evidence to support this statement.

[a]The citations in these quotes have been altered to make them consistent with the style used in this article. The text formatting (e.g. use of subscript, italics) used in quotes is otherwise unchanged.

rapid growth in herbaceous/grass species (Atkinson et al., 2016). However, C_4 trees are notably rare: The only known true C_4 trees are members of *Euphorbia* (Euphorbiaceae) and are endemic to the Hawaiian Islands, where they evolved from a single common herbaceous ancestor (Yang & Berry, 2011; Young et al., 2022). Unlike their herbaceous counterparts, these rare C_4 trees are not known to have fast growth rates and do not exceed 10 m in height (Sporck, 2011; Yang et al., 2018; Young et al., 2020). The short stature and slow growth of these Hawaiian C_4 trees are in opposition to the idea that C_4 photosynthesis may be responsible for the rapid growth of Paulownia trees.

There are several key physiological and anatomical parameters that differ between plants utilising the C_3 and C_4 photosynthetic pathways, and these parameters can be measured to conclusively establish photosynthetic type (Table 2). The reason why C_3 and C_4 plants differ in these key parameters can be understood by examining the numerous biochemical and anatomical differences between the ancestral C_3 and derived C_4 states (*reviewed in* Sage, 2004). In C_3 plants, chloroplasts containing Rubisco (the carbon-fixing enzyme) are numerous in the mesophyll tissue (Stata et al., 2014), and it is here that CO_2 from the atmosphere is fixed. Conversely, in C_4 plants, chloroplasts, and thus Rubisco, are much less abundant in the mesophyll and it is a different enzyme—PEPC (phosphoenolpyruvate carboxylase)—which captures CO_2 here (Chollet et al., 1996; Kanai & Edwards, 1999; Perrot-Rechenmann et al., 1982). Carbon is then shuttled into the bundle sheath (the tissue that surrounds the veins) where the chloroplasts are located. This shuttling mechanism acts to concentrate CO_2 around Rubisco in the bundle sheath of C_4 plants, increasing the efficiency of carbon fixation. The greater importance of bundle sheath tissue to photosynthesis in C_4 compared with C_3 plants results in observable anatomical differences between the two types (Figure 2). In particular, C_4 leaves typically have higher vein density and less mesophyll tissue compared with C_3 leaves, and their chloroplasts are localised primarily in the bundle sheath tissue rather than the mesophyll (Dengler & Nelson, 1999; Lundgren et al., 2014, 2019; Stata et al., 2014).

In addition to these anatomical differences, C_4 leaves also present different physiology than C_3 leaves, and it is these physiological traits which are definitive when identifying C_4 photosynthesis. In particular, C_4 plants are characterised by their lower CO_2 compensation points (CCP, i.e. the intercellular concentration of CO_2 at which net photosynthesis is zero because the CO_2 taken in by photosynthesis is equal to that released by respiration and photorespiration), higher carboxylation efficiencies (CEs, i.e. the rate of net carbon fixation per unit CO_2 available to be fixed within the leaf) and higher water use efficiencies (WUEs, i.e. the amount of net carbon assimilated per unit of water used) compared with their C_3 counterparts (Kanai & Edwards, 1999; Long, 1999). These differences result from the C_4 carbon shuttle's ability to effectively concentrate CO_2 around Rubisco. Given Rubisco can catalyse the addition of both CO_2 and O_2; its CE is reduced when oxygenation occurs. The concentration of CO_2 around Rubisco in C_4 plants virtually eliminates oxygenation, and consequently, the energetically costly process of photorespiration, resulting in distinctly lower CCP and higher CE in C_4 plants compared with C_3 plants (Dai et al., 1996; Kanai & Edwards, 1999; Lundgren et al., 2016). Furthermore, the operation of the C_4 shuttle facilitates the maintenance of higher rates of photosynthesis at lower internal CO_2 concentrations (requiring lower rates of stomatal conductance and thus water loss via transpiration) in C_4 versus C_3 plants, resulting in higher WUE (Long, 1999; Osborne & Sack, 2012).

Plants using C_3 versus C_4 photosynthesis can also be distinguished effectively using stable isotope discrimination (Cernusak et al., 2013; Von Caemmerer et al., 2014). The different mechanisms of CO_2 fixation between C_3 and C_4 plants result in distinct $\delta^{13}C$

TABLE 2 Criteria for determining photosynthetic type

Parameter	Units	Photosynthetic type		Citation
		C_3	C_4	
Anatomical variables				
Chloroplast localization	-	Mostly M[a]	Mostly BS[b]	Pearcy and Franceschi (1986)†‡; Stata et al. (2014)
Interveinal distance	μm	≳ 130	≲ 130	McKown and Dengler (2007); Griffiths et al. (2013)
Physiological variables				
CO_2 compensation point	μmol mol^{-1}	> 35	≤ 5	Pearcy and Calkin (1983)†‡; Dai et al. (1996)†‡
Carboxylation efficiency	mol m^{-2} s^{-1}	≤ 0.15	> 0.15	Lundgren et al. (2016) Dai et al. (1996)†‡
Water use efficiency	mmol mol^{-1}	≤ 100	> 100	Pearcy and Franceschi (1986)†‡; Osborne and Sack (2012)
$\delta^{13}C$	‰	≤ − 22	≥ − 14	Pearcy and Troughton (1975) ‡; Cernusak et al. (2013)†

Note: Typical values for C_3 and C_4 species are shown, as determined from the literature. Typical values for C_3 and C_4 species are obtained primarily from data on eudicot herbs, and secondarily grasses, but are supported with data from woody species where possible, as indicated by citations marked with † for C_3 species and ‡ for C_4 species.

[a]Mesophyll.

[b]Bundle Sheath.

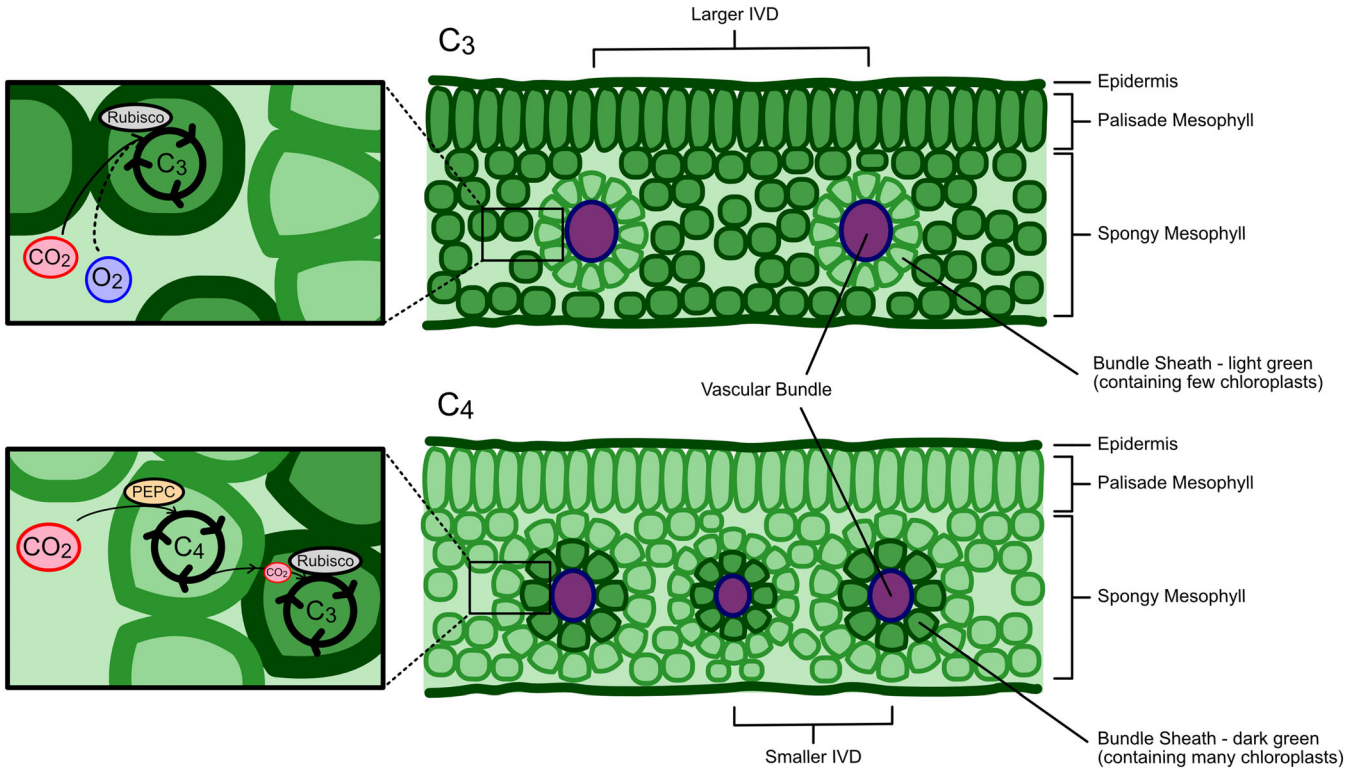


FIGURE 2 Illustration of the differences between typical C_3 and C_4 leaf anatomy and biochemistry. Cells containing many chloroplasts (i.e. the mesophyll cells in the C_3 illustration and the bundle sheath cells in the C_4 illustration) are shown in dark green. Cells containing few chloroplasts are shown in light green. The vascular bundle is shown in purple. The expanded sections show the localisation of the C_3 and C_4 cycles within the different tissue types. In C_3 leaves, the C_3 cycle is localised to the dark green mesophyll tissue. In C_4 leaves, the C_4 cycle is localised to the light green mesophyll tissue, and carbon is shuttled to the C_3 cycle, which is localised in the dark green bundle sheath tissue. IVD, interveinal distance; PEPC, phosphoenolpyruvate carboxylase.

signatures of leaf tissue, as Rubisco favours the abundant ^{12}C isotope and strongly discriminates against the heavy ^{13}C isotope. Given that C_3 plants initially fix CO_2 via Rubisco, they fix a lesser proportion of $^{13}CO_2$ than C_4 plants and, as such, have very negative leaf $\delta^{13}C$ signatures (< −22‰ for well-watered tree seedlings, Cernusak et al., 2013). C_4 plants, which use PEPC and not Rubisco for the initial fixation of CO_2, fix a greater proportion of $^{13}CO_2$, resulting in less negative leaf $\delta^{13}C$ signatures, typically between −11‰ and −14‰ (Cernusak et al., 2013; Von Caemmerer et al., 2014). The Hawaiian C_4 trees are typical in this regard, with $\delta^{13}C$ signatures ranging from −12.4‰ to −14.4‰ (Pearcy & Troughton, 1975). As such, measuring the key leaf anatomical, physiological and isotopic parameters discussed above is both necessary and sufficient to identify the presence of the C_4 photosynthetic pathway.

Only one attempt has so far been made to collect any of these data regarding the photosynthetic type of Paulownia, with the study in question concluding that Paulownia does not use C_4 photosynthesis (Cao et al., 2021). However, we feel that the data Cao et al. have collected were not sufficient relative to the standard laid out above to support photosynthetic characterisation. As such, in this study, we have set out to conclusively determine the photosynthetic type of Paulownia trees by analysing leaf anatomy, physiology and stable isotope evidence in three species. In order for a given species to be classified as using C_4 photosynthesis, the value of each measured parameter was required to lie within the range of expected values for C_4 species laid out in Table 2. We show that none of the three species in this study, *P. tomentosa*, *Paulownia fortunei* and *Paulownia kawakamii*, meet our criteria to be classified as a C_4 species. This finding is used to demonstrate that the claim that Paulownia uses C_4 photosynthesis has arisen from poor citation practices rather than scientific evidence.

2 | MATERIALS AND METHODS

2.1 | Geographical distribution

To characterise the geographical distribution of *Paulownia* species, occurrence data were downloaded from the Global Biodiversity Information Facility (GBIF.org, accessed 12 January 2022) for all species in *Paulownia*. These data were then processed in R (R Core Team, 2021) to remove records without coordinates or with potentially inaccurate coordinates. Specifically, data were processed using the CoordinateCleaner package in R to identify and remove records with coordinates that designated country capitals or centroids, the GBIF headquarters or a biodiversity institution; records with equal, zero or invalid values for latitude and longitude; and records with coordinates that denoted an area in the sea

(Zizka et al., 2019). Finally, all coordinate data were rounded to two decimal places and duplicate records (i.e. records for the same species with matching coordinates) were removed. After these cleaning steps, 10,698 occurrence records for eight species remained.

2.2 | Plant material

Seeds were obtained for three species in genus *Paulownia*: *P. tomentosa* from Tree Seed Online Ltd (www.treeseedonline.com) and *P. fortunei* and *P. kawakamii* from Mark Davies Seeds (www.markdaviesseeds.com). Seeds were germinated on the surface of moist John Innes No. 2 compost (Westland, County Tyrone, Northern Ireland) in seed trays under a clear plastic cover, which was removed after germination. Once seedlings reached approximately 5–10 cm tall, they were transplanted into 3-L round plastic pots containing the same type of compost. Seedlings were confirmed to be consistent with published characterisations of the species as far as possible given that plants could not be maintained through to flowering (Hu, 1961). Throughout germination and growth, plants were kept well-watered and under conditions of ambient CO_2, 24/18°C day/night temperatures and a 16-h photoperiod from 06:00 to 22:00 where photosynthetic photon flux density (PPFD) was maintained between 200 and 600 μmol m^{-2} s^{-1} in a greenhouse at Lancaster University, UK.

2.3 | Physiology

Leaf physiology measurements were made on the youngest fully expanded leaf of five replicate plants of each species 2- to 4-months post-germination using the LI-6800 portable photosynthesis infrared gas analyser system (LI-COR, Lincoln, NE, USA). All measurements were made between 09:00 and 17:00. CO_2 response curves were collected for five replicate plants per species at 28°C leaf temperature, 300 μmol^{-1} flow rate, 55% relative humidity and a saturating light level (confirmed to be 1000 μmol m^{-2} s^{-1} for all three species) after a minimum of 30 min of acclimation to chamber conditions, during which time rates of CO_2 and H_2O exchange stabilised. Subambient CO_2 response curves were collected at decreasing values of CO_2r of 400, 300, 200, 150, 100, 75, 50, 25 and 5 μmol mol^{-1}, with measurements taken after rates of CO_2 and H_2O exchange had stabilised at each CO_2 concentration. A regression line was fitted through points falling along the initial linear portion of each CO_2 response curve. CE was calculated as the slope of this regression line, while the CCP was calculated as the x-intercept. WUE was calculated as the rate of net assimilation at 400 μmol mol^{-1} CO_2 (A_{400}), divided by the value for stomatal conductance (g_s) collected at the same point.

2.4 | Carbon isotope analysis

Following physiology measurements, the measured leaves were harvested for carbon isotope and anatomy analyses. Half of each leaf was dried for a minimum of 1 week in a drying oven. Equal masses of dried leaf material were taken from each sample and combined to create a single pooled sample for each species. Leaf material was then ground into a homogenous powder using a mixer mill (MM 400, Retsch, Haan, Germany) then 450–550 μg of ground leaf material per pooled sample was weighed into individual 8 mm × 5 mm tin capsules (Elemtex Ltd, Cornwall, UK). $\delta^{13}C$ signatures, presented as isotopic ratios (per mil, ‰) relative to the isotopic standard Vienna PeeDee Belemnite, were determined using a Costech Elemental Analyser attached to a Thermo DELTA V mass spectrometer via a Conflo IV in continuous flow mode (Thermo Fisher Scientific, Waltham, MA, USA) at the Godwin Laboratory, University of Cambridge.

2.5 | Anatomy

Leaf tissues from freshly harvested leaves were used for fresh and embedded leaf anatomical analyses. For preparation of fresh cross-sections, leaf samples of approximately 6 mm^2 were taken from the central area of each leaf (avoiding the midrib and leaf edges) and placed in distilled H_2O. These samples were sectioned by hand using a fresh razor blade and mounted onto standard microscope slides with distilled H_2O and a cover slip. Fresh leaf sections were imaged at 40X magnification using a Leica DMC4500 digital microscope camera mounted onto a Leica DM2500 LED microscope (Leica Microsystems, Wetzlar, Germany) to characterise chloroplast localisation (i.e. in mesophyll vs. bundle sheath tissue).

For preparation of embedded cross-sections, leaf samples of approximately 2 × 5 mm in size were taken from each leaf and fixed via vacuum infiltration in a 4:1 solution of 100% EtOH: 99% glacial acetic acid, then stored in the dark in a 4°C fridge for a minimum of 24 h. Samples were then sequentially dehydrated in EtOH and embedded in Technovit 7100 methacrylate resin (Heraeus Kulzer GmbH, Wehrhein, Germany). Embedded samples were then sectioned 6–8 μm thick on a HistoCore MULTICUT R semi-automated rotary microtome (Leica Biosystems, Wetzlar, Germany), dried onto microscope slides, stained with 0.1% Toluidine blue O (TAAB Laboratories Equipment Ltd, Berkshire, UK) in 0.2 M pH 7.0 phosphate buffer (Alfa Aesar, Heysham, UK), then permanently mounted with DPX mountant (TAAB Laboratories Equipment Ltd, Berkshire, UK). Using the same microscopy set-up as above, cross-section images were acquired at 10X magnification. Images were analysed using ImageJ software (version 1.53 k, National Institutes of Health, USA) to measure the interveinal distance (IVD) i.e. the distance between the central points of consecutive vascular bundles as shown in Figure S1.

3 | RESULTS

3.1 | Global distribution of paulownia

GBIF occurrence data suggest that Paulownia is widespread in its native range of East Asia, particularly in South Korea ($n = 477$), China ($n = 350$)

and Japan ($n = 172$). It has also spread into, and become abundant in, many European countries including France ($n = 3207$), Switzerland ($n = 695$) and Italy ($n = 614$) and is present in 39 of the 50 US states ($n = 2885$), being found most commonly in the Eastern United States (Figure 1). It is less widespread in the Southern Hemisphere, with fewer than 100 occurrences recorded in any country south of the equator, including Australia ($n = 28$) and New Zealand ($n = 79$), although this may relate to reduced sampling effort rather than true absence. Within the genus, *P. tomentosa* is, by far, the most abundant species, with a global distribution representing 10,316 of the 10,698 occurrence records (Figure 1). *P. fortunei* ($n = 154$) and *P. kawakamii* ($n = 105$) are the only other species with more than 100 occurrences recorded. Two of the eight species—*P. henanensis* ($n = 2$) and *P. taiwaniana* ($n = 31$)—are found only in their native range in East Asia. Two of the remaining three species—*P. catalpifolia* ($n = 15$) and *P. elongata* ($n = 15$)—are found only in China and New Zealand, while *P. fargesii* ($n = 60$) is found only in China and Norway.

3.2 | Leaf physiology and stable carbon isotopes

Measurements of leaf physiology in all three *Paulownia* species in this study were not consistent with C_4 photosynthesis (Tables 2 and 3). The shapes of the subambient CO_2 response curves (Figure 3) were typical of a C_3 species, with shallow initial slopes (i.e. low CE). Indeed, the values of CE were less than 0.15 mol m^{-2} s^1 for all the three species, consistent with C_3 photosynthesis. CCPs were also consistent with that of C_3 species, being lowest in *P. fortunei* (55.67 μmol mol^{-1}) and highest in *P. tomentosa* (63.81 μmol mol^{-1}). WUE ranged from 68.20 mmol mol^{-1} in *P. fortunei* to 103.02 and 104.54 mmol mol^{-1} in *P. kawakamii* and *P. tomentosa*, respectively (Table 3). The latter two values are on the higher end of what would be considered typical for a C_3 species (Table 2) but nevertheless are still consistent with the finding that Paulownia does not use C_4 photosynthesis.

Further supporting this conclusion, $\delta^{13}C$ signatures of leaf tissue from all three species were < −22‰, with values ranging from −22.22‰ in *P. tomentosa* to −25.59‰ in *P. fortunei* (Table 3). These values are much more negative than would be typically observed in a C_4 species (Table 2).

3.3 | Leaf anatomy

Anatomically, none of the three *Paulownia* species meet the criteria to be considered a C_4 species (Tables 2 and 3 and Figure 4). Fresh leaf

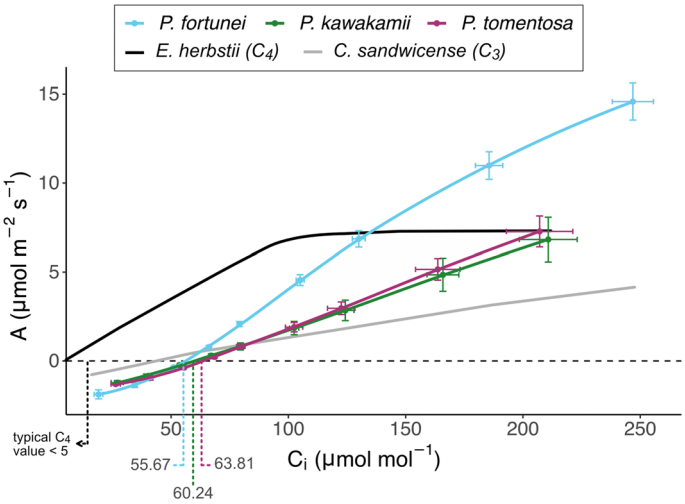


FIGURE 3 Leaf physiology of *Paulownia fortunei*, *Paulownia kawakamii* and *Paulownia tomentosa* compared with the physiology of C_3 and C_4 tree species. Steady-state net photosynthetic CO_2 assimilation (a) was measured at a range of substomatal CO_2 concentrations (C_i) for five replicate plants of each of the three species in *Paulownia*. The mean of these five replicate curves was calculated for each species to give a mean A-C_i curve per species, which is shown alongside example curves for a C_3 (*Claoxylon sandwicense*) and C_4 (*Euphorbia herbstii*) tree species. Error bars show the standard error of A and C_i at each point on the mean curves. The value of C_i at which net assimilation is zero (i.e. the carbon compensation point) is indicated for each species, with the typical value for a C_4 species also indicated. Data for the C_3 and C_4 comparison tree species were obtained from Figure 3 of Pearcy and Calkin (1983).

TABLE 3 Summary of physiological and leaf anatomical data obtained from species in *Paulownia*

Parameter	Units	Species		
		Paulownia tomentosa	*Paulownia fortunei*	*Paulownia kawakamii*
Anatomical variables				
Chloroplast localisation	-	Mostly M[a]	Mostly M[a]	Mostly M[a]
Interveinal distance	μm	156.34 ± 11.16	225.13 ± 15.64	181.52 ± 13.58
Physiological variables				
CO_2 compensation point	μmol mol^{-1}	63.81 ± 1.76	55.67 ± 0.99	60.24 ± 1.96
Carboxylation efficiency	mol m^{-2} s^{-1}	0.05 ± 0.01	0.09 ± 0.00	0.04 ± 0.01
Water use efficiency	mmol mol^{-1}	104.54 ± 8.95	68.20 ± 5.51	103.02 ± 8.54
$\delta^{13}C$	‰	−22.22	−25.59	−23.18

Note: Mean ± standard error (2 d.p.) is shown for each of the continuous parameters measured for *Paulownia tomentosa*, *Paulownia fortunei* and *Paulownia kawakamii* ($n = 5$). A single $\delta^{13}C$ value was measured from a pooled sample for each species.
[a]Mesophyll.

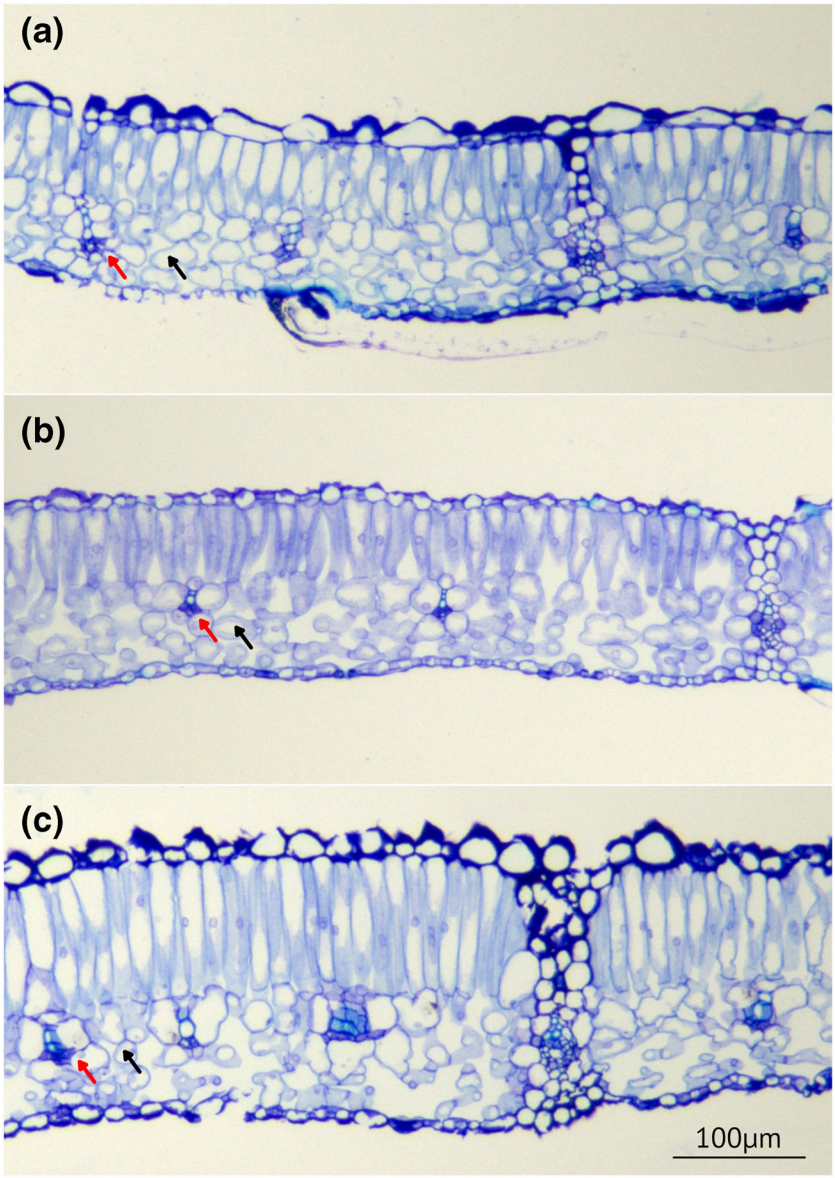


FIGURE 4 Cross-sectional leaf anatomy of (a) *Paulownia tomentosa*, (b) *Paulownia fortunei* and (c) *Paulownia kawakamii*. One representative light micrograph of a fixed leaf cross-section is shown per species, imaged at 10× magnification. Red arrows indicate bundle sheath cells; black arrows indicate mesophyll cells. Note the distance separating vascular bundles, referring to Figure S1 for measurement details

cross-sections from all three species showed abundant chloroplasts in mesophyll cells, with few or no chloroplasts in the bundle sheath tissue around the veins (Figure S2). All three species presented long distances between vascular bundles: the smallest IVD, found in *P. tomentosa* (156.34 μm), was still higher than would be expected in the presence of C_4 photosynthesis (Tables 2 and 3).

4 | DISCUSSION

4.1 | Paulownia trees do not use C_4 photosynthesis

The findings from all three lines of evidence investigated in this study—leaf physiology, stable carbon isotopes and leaf anatomy—are inconsistent with a C_4 phenotype being present in any of the three species measured. The leaf physiology and stable carbon isotope data in particular strongly contradict the idea that Paulownia uses C_4 photosynthesis as the values for CCP and $\delta^{13}C$ are very different from typical C_4 values (Tables 2 and 3). Indeed, the values of CCP seen in all three species are much higher than what is typically observed for a C_4 plant (≤ 5) and are indicative of a higher rate of photorespiration than would be expected for a C_4 plant. Similarly, low values of CE in all species indicate that the efficiency of carbon fixation is not being increased by a carbon concentrating mechanism. The very negative $\delta^{13}C$ signatures of < −22‰ in each species indicate a high level of discrimination against heavy isotope carbon, meaning that it is likely that the vast majority of initial CO_2 fixation is occurring via Rubisco and not via PEPC. This is not compatible with C_4 photosynthesis.

With regard to leaf anatomy, chloroplasts are localised primarily to the mesophyll, indicating that CO_2 fixation via Rubisco is occurring here, rather than in the bundle sheath, which has insufficient chloroplast concentration to sustain photosynthesis (Table 3 and Figure S2). The paucity of chloroplasts in the bundle sheath precludes the establishment of a carbon shuttle, as would be observed in C_4 plant.

The conclusion that Paulownia trees do not use C_4 photosynthesis is the same one reached by Cao et al. (2021) in their study of witches' broom in *P. fortunei*. However, the evidence provided by Cao et al. to support their (correct) conclusion was insufficient relative to the typically accepted standard for characterising the photosynthetic type of a species (e.g. Lundgren et al., 2016; Marshall et al., 2007; Sage et al., 2011). Net photosynthetic rate was measured but only under a single (unspecified) set of conditions rather than across a range of CO_2 concentrations, which means that the CCP cannot be established. Leaf anatomy was presented as an image of a single major vein, rather than looking across multiple veins for the decreased IVD or vein density which is characteristic of a C_4 species (Table 2). Similar to our study, Cao et al. measured $\delta^{13}C$ values in *P. fortunei* to be far more negative than those expected for a C_4 plant (−32‰ to −34‰). These $\delta^{13}C$ values are much more negative than those measured in our study. While very negative $\delta^{13}C$ values can indicate double discrimination against the heavier ^{13}C isotope as a result of a glycine shuttle (Von Caemmerer, 1992), our anatomy and physiology data are not consistent with Paulownia using C_2 photosynthesis (Lundgren et al., 2016; Sage et al., 2011). Instead, the high level of carbon isotope discrimination identified in Cao et al.'s study is likely linked to the environmental conditions during plant growth, as discrimination is greater given an abundant supply of water and exposure to low photon flux density (Cernusak et al., 2013). Additionally, high levels of anthropogenic air pollution (such as those found in Zhengzhou, where these Paulownia were grown) can also result in more negative $\delta^{13}C$ values than those from plants grown in a low-pollution area, although this effect is not consistent in trees (Pataki et al., 2010). Addressing the suggestion made in a recent study (Wang et al., 2019) that Paulownia may also employ crassulacean acid metabolism (CAM) in addition to C_3 photosynthesis, Cao et al. (2021) conclude that it is the integration of C_3 with CAM metabolism that is responsible for the rapid growth rate in Paulownia. However, we believe that further studies are needed to confirm this physiological characterisation: Our data cannot rule out the possibility of facultative CAM which is only induced under drought stress.

4.2 | The C_4 photosynthesis myth in Paulownia has arisen from inaccurate citations

Our data show that the idea that Paulownia uses the C_4 photosynthetic pathway is not supported by scientific evidence. The origin of this misinformation is not clear, although inaccurate citation practices have certainly played a role in perpetuating the myth (Table 1). One possible source of confusion is that C_3 plants have so-called 'C_4 enzymes' which do not act as components of a C_4 carbon concentrating mechanism but may have other roles in the leaf, for example, during stress responses (Doubnerová & Ryšlavá, 2011). Ivanova et al. (2016) discuss a possible role for C_4 enzymes in Paulownia in tolerance to salinity, suggesting that these enzymes (including PEPC) increase in activity under salt stress. It is possible that C_4 cycle enzymes in Paulownia, while not part of a C_4 photosynthetic pathway, could have a role in facilitating the rapid growth of these trees, but this idea has not been scientifically investigated.

The C_4 photosynthesis story in Paulownia is indicative of a wider problem of inaccurate citations in this body of literature. This is evidenced by further examples of missing citations: Paulownia seeds being used as packing material for porcelain exporters as a mechanism for the introduction of Paulownia to the United States and Europe is an idea that is widely shared within the literature (Del Tredici, 2010; Yadav et al., 2013), but in each of the examples cited here, the idea goes either totally uncited or accompanied by a citation to a secondary source. To be clear, best practice for citation stipulates that authors should always strive to support their statements with either a reference to primary literature, that is, peer-reviewed journal articles, books and reports that present original research data, or alternatively first-hand accounts and observations, rather than literature reviews ('Credit where credit is due', 2009; 'On citing well', 2010). However, as is apparent here, best practice in citation is not always, and perhaps cannot always be, enforced by editors even in peer-reviewed publications, which facilitates the persistence of these myths in the literature on Paulownia. Failure to acknowledge instances where statements are poorly supported by a given citation or citing findings without critically assessing the potential shortcomings of the reference in question can legitimise claims that may or may not be true and impair the ability of the reader to critically evaluate the information presented (Penders, 2018).

Unfortunately, the citation practices exhibited in the body of literature on Paulownia appear to be symptomatic of a wider problem within academia of inaccurate citations (*reviewed in* Hosseini et al., 2020). Most relevant to the story presented here, Hosseini et al. highlight an analysis by Todd et al. (2007) that suggests that almost 25% of citations in ecology failed to 'clearly support' the assertion made by the author. Todd et al. (2007) attribute the prevalence of miscitation, in part, to increasing demands on scientists to publish, an idea that is supported in the editorial 'Credit where credit is due' (2009), which points towards an increased reliance on review literature (rather than primary literature) among researchers who are 'chronically short of time'. This is perhaps ironic given that inaccurate citations themselves can contribute to research waste (Hosseini et al., 2020) by making it more difficult for researchers to critically assess the existing literature on a topic and identify knowledge gaps that merit further research.

4.3 | Poor citation practices can have real-life consequences

It is important to acknowledge that poor citation practices, and their implications for the dissemination of scientific knowledge, have impacts that reach beyond the scientific community. Many of the studies and organisations that suggest Paulownia uses C_4 photosynthesis (Table 1) are proposing new potential uses for Paulownia. Most concerning are those organisations that state that Paulownia is C_4 to legitimise investing in this tree for the purpose of carbon offsetting.

For example, the research consultancy Thunder Said Energy (thundersaidenergy.com, accessed on 28 April 2022) investigates the potential for *P. tomentosa* as a 'nature based solution to climate change' and repeats the myth that Paulownia is a C_4 plant (although they do show scepticism regarding the true CO_2 uptake rate of Paulownia plantations and express concerns about its invasiveness). Thunder Said Energy point potential investors to one of the major growers of Paulownia globally, WorldTree (www.worldtree.eco, accessed on 28 April 2022), who claim that Paulownia uses 'a unique and powerful type of photosynthesis … found in only about 3% of all land plants, including some grasses like corn and sugarcane.' Given that maize and sugarcane utilise the C_4 pathway, the implication is clear here, even if it is not stated explicitly. WorldTree also suggests that Paulownia has nitrogen-fixing leaves that can return nitrogen to depleted soil, information which seems to have been derived from a report prepared by NatureBank on WorldTree's behalf (NatureBank., 2019). This NatureBank report engages with the scientific literature, in particular two papers by Icka et al. (2016) and Woźniak et al. (2018) which both mistakenly state that Paulownia utilises the C_4 pathway (Table 1). This establishes a direct link between miscitations in the literature and misinformation being shared with potential investors.

The misinformation rife in the literature and online regarding Paulownia makes it very difficult to critically assess whether or not Paulownia is a worthwhile investment. It seems likely that the potential for carbon sequestration and the ecologically robust nature of Paulownia have been, in many cases, wildly overstated. When investors fall victim to an overestimation of the potential of Paulownia, the consequences can be devastating. The Australian Broadcasting Corporation reported in 2015 that Paulownia investment schemes have cost 'thousands of Australian investors their life savings' (Bembridge, 2015). Additionally, there are ecological concerns regarding the potential invasiveness of Paulownia that should be carefully considered by any organisation advocating for or permitting the establishment of Paulownia plantations.

4.4 | Concluding remarks

Despite the confusion generated by miscitation and misinformation, it remains true that Paulownia is a culturally and economically significant tree whose timber has many potential uses (Hu, 1961; Zhu et al., 1986). This potential means that Paulownia timber is highly valuable, particularly in Japan, which is somewhat amusingly illustrated by a series of thefts of Paulownia trees from Fairmount Park in Philadelphia in the 1980s to 1990s, for sale on the 'black market' (Butler, 1984; Cipriano, 1987; Gillin, 1990). In order to establish the potential for any novel uses of Paulownia, the carbon sequestration capacity, nitrogen-fixing capability and potential for invasive establishment of these trees need to be assessed in peer-reviewed research by nonbiassed parties. Additionally, the assumption that Paulownia utilises C_4 photosynthesis, resulting in its rapid growth, has meant that there has been little attempt made to understand why Paulownia is indeed so fast-growing. This merits further research to establish the true mechanism behind the rapid growth of Paulownia.

ACKNOWLEDGEMENTS

We thank Freya Cook and Catherine Walsh for assistance with data collection, James Rolfe from the Godwin Laboratory, University of Cambridge, for carbon isotope analysis and Britta Krümpers for making the authors aware that Paulownia has been considered a C_4 plant in the literature. SNRY is funded by a Natural Environment Research Council Envision Doctoral Training Partnership studentship (NE/S007423/1) and MRL is funded by a UK Research and Innovation Future Leaders Fellowship (MR/T043970/1).

CONFLICT OF INTEREST

The authors report no conflict of interest.

AUTHOR CONTRIBUTION

SY collected the data. SY and ML conceptualised the study and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Occurrence data used in this study are available from the Global Biodiversity Information Facility (GBIF, https://doi.org/10.15468/dl.bc6bus). All other data that support the findings of this study are available from the Lancaster University Research Directory (https://doi.org/10.17635/lancaster/researchdata/536).

ORCID

Sophie N. R. Young https://orcid.org/0000-0002-5080-2904
Marjorie R. Lundgren https://orcid.org/0000-0002-2489-3646

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Young, S. N. R., & Lundgren, M. R. (2023). C_4 photosynthesis in *Paulownia*? A case of inaccurate citations. *Plants, People, Planet*, *5*(2), 292–303. https://doi.org/10.1002/ppp3.10343