



Full Length Research Article

Morphoanatomical Responses and Stomatal Conductance in Shaded and Sun-Exposed *Broussonetia papyrifera* Seedlings

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ABSTRACT

Investigating invasive species' morphoanatomical characteristics, such as leaf area and thickness of vascular tissues and storage cells, can reveal information about their adaptive ability and competitive advantage. Thus, we analyzed the variation in leaf, stem, and root morphoanatomical structure and stomatal conductance between shaded and sun-exposed seedlings of *Broussonetia papyrifera* to provide insights into management strategies to control its invasive ability. The variations in leaf area (LA), Leaf Mass per Area (LMA), stomatal density, thickness of palisade and spongy mesophyll tissues, thickness of xylem parenchyma cells, diameter of all xylem vessels in stem and roots and stomatal conductance were analyzed between shaded and sun-exposed seedlings. Results revealed that the LA and LMA of *B. papyrifera* were significantly larger in the sun-exposed than in the shaded condition. Seedlings exposed to sunlight also had thicker palisade mesophyll and xylem parenchyma cells. The diameter of xylem vessels in roots was also significantly higher in sun-exposed seedlings. Contrarily, a reverse pattern was observed in the diameter of stem xylem vessels (i.e., shaded > sun-exposed seedlings). Physiologically, a higher stomatal conductance was also observed in sun-exposed seedlings. In conclusion, we found significant variations in leaf, stem, and root morphoanatomy and stomatal conductance between shaded and sun-exposed seedlings of *B. papyrifera*. The findings of the present study may provide valuable implications for managing or controlling its invasibility in the introduced range.

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1. Introduction

Invasive species are a major element of global change and pose an increasing impairment of forest ecosystems worldwide (Handayani et al. 2023; Pyšek and Richardson 2010). Although not all non-native plant species are invasive, many of them can outcompete native species, disrupt nutrient cycling, reduce global and local biodiversity, and consequently affect plant community structure, causing great environmental harm to the invaded area (Brancalion et al. 2019; Pearson et al. 2018). Biological invasions also have serious socioeconomic and health consequences (Roy et al. 2019). Climate change exacerbates the problem by creating favorable conditions for invasive species to establish and spread and is likely to influence competitive interactions between native and invasive species (Finch et al. 2021; Walther et al. 2009). Ecologists, however, have long

proposed that instead of being eliminated, invasive plant species can be utilized for ecosystem restoration of degraded lands (Pandey 2012). Several policies and risk assessments are also currently in place to control the adverse effects of invasive species in forest ecosystems (Pötzelsberger et al. 2020). Hence, studies on methodologies (e.g., prevention, integrated pest management, mechanical/physical control, chemical control, and biological control) to effectively eradicate invasive plants have been very evident in the last decades (D'Antonio et al. 2016). Although solutions to control invasive plant species have long been tested for some plants, the decision on which appropriate method to use still depends on several factors, including invasive plant species' growth forms, local economic conditions, and available control resources (Weidlich et al. 2020). Their practicality, economic feasibility, and ease of implementation may also vary depending on the species and circumstances. Thus, further research on how every invasive plant species responds and interacts with the changing environment is necessary to help improve the development of control efforts amid a changing environment.

Invasive species' competitive ability against native species may be context-dependent as competitive strength varies depending on environmental gradients, e.g., light intensity (Čuda et al. 2015). For example, these species can be more prevalent in open areas, where resource supply is high, due to favorable conditions such as increased sunlight, fewer competitors, and less shading (Silvertown and Charlesworth 2009). This tendency enables them to establish and spread rapidly, outcompeting native species. However, certain invasive plant species can also thrive in closed ecosystems or forested areas, utilizing adaptations to compete effectively in shaded environments. For example, shading treatment drove the distribution of an invasive *Impatiens* species in some regions (Čuda et al. 2013), suggesting that invasive species can exhibit varying responses to different light conditions. Some invasive species are shade-tolerant and can thrive in low-light environments, while others are adapted to high-light conditions and show increased growth in full sunlight. An experiment, for instance, reported better growth performance of an invasive species, *Phytolacca americana*, in a low-light environment, although field observations suggest that the species can also grow in open habitats (Xiao et al. 2022). Shade tolerance in the invasive plant *Solidago canadensis* was also associated with its successful establishment in a particular area, as cited in Xiao et al. (2022). Previous research suggests that distinct patterns of plant growth and reproduction of invasive plant species contribute to their successful invasion of new environments because their growth advantage is frequently attributed to adaptations, adaptability, and efficient light uptake. Thus, understanding these dynamics is crucial for managing invasive plant species and maximizing their positive ecological benefits.

Morphoanatomical responses of invasive plant species, such as leaf features, root systems, and growth patterns, shed light on their adaptive strategies and competitive advantage in the introduced range (Ilyas et al. 2022). Plant functional traits enhance resource acquisition, colonization, and competitive abilities, explaining invasive species' performance within an invaded area (Kaushik et al. 2022). Leaf size, for example, is an important functional leaf trait that accurately characterizes the plant's resource-use strategy in response to changes in available resources (Scheepens et al. 2010; Wang et al. 2016). Moreover, a study discovered unique leaf anatomical traits in several invasive plant species, including sclerenchymatous tissue thickness and vascular bundle area, implying that anatomical traits significantly predict plant invasiveness (Rindyastuti et al. 2021). Physiologically, studying stomatal conductance in invasive species provides insights into their water use efficiency, photosynthetic capacity, and adaptability to different environmental conditions (Hernandez et al. 2022). A meta-analysis reported a strong

tendency for invasive species to have greater stomatal conductance than other non-invasive species (Cavaleri and Sack 2010). Because of a complex network of structural and physiological traits, high stomatal conductance suggests a competitive advantage for plants, including invasive ones, in resource-limited environments. Understanding these responses will thus aid in assessing species' invasive potential, predicting their impact, and guiding management strategies, especially given that managing invasive species is becoming increasingly difficult and expensive as new populations of invasive plants spread and reach high densities (Venette et al. 2021).

Paper mulberry (*Broussonetia papyrifera*) is a tree species native to Asia (from continental East Asia to the Polynesian islands). The species is known for its fast growth, adaptability to various environments, and high seed production; hence, it is deemed an economically important plant in paper production (Seelenfreund et al. 2010). However, it has become an invasive species in many parts of the world, including Argentina, Ghana, Uganda, Pakistan, Philippines, Solomon Islands, and USA, where it can outcompete native vegetation and disrupt natural ecosystem dynamics (Barker 2002; Bosu et al. 2013; Chung et al. 2017; Marwat et al. 2010). Studying the morphological and anatomical characteristics of *B. papyrifera* between shaded and sun-exposed seedlings is important in elucidating invasiveness. Understanding its adaptation to different light environments may provide insight into its success in any new environment. Researchers can develop effective control management strategies by identifying specific traits that contribute to invasiveness. Consequently, this study analyzed the variation in leaf, stem, and root morphoanatomical structure and stomatal conductance between shaded and sun-exposed seedlings of *B. papyrifera* and provided insights into management strategies to control its invasive ability. It was hypothesized that the leaf, stem, and root morphoanatomical characteristics and stomatal conductance would vary significantly between shaded and sun-exposed seedlings. Specifically, this study expected that the shade seedlings would exhibit specific morphoanatomical adaptations to optimize stomatal conductance.

2. Materials and Methods

2.1. Source of Plant Materials

Approximately one-year-old seedlings of *B. papyrifera* were collected from two locations: (1) under the forest canopy, hereafter referred to as shaded, and (2) forest gap, hereafter referred to as sun-exposed, in Mount Makiling Forest Reserve (MMFR) at 520-560 meters above sea level (Fig. 1). The shaded area has a relatively lower light intensity (i.e., 595 to 1350 lux) than sun-exposed (i.e., 8000 to 10000 lux) because of the dense foliage trees that limit the amount of sunlight that can pass through the forest floor. The shaded area is dominated by various large and mature tree species, including Dipterocarps (e.g., *Shorea contorta*), *Vitex parviflora*, and *Lagerstroemia speciosa*. The sun-exposed had an approximately 1.5 m to 2 km canopy gap, with some seedlings of trees, shrubs, and even grasses/weeds growing within the gap.

2.2. Morphoanatomical Traits Measurement

Young leaf, stem, and root samples were collected from four healthy seedlings planted under the shaded and sun-exposed areas. Samples were first stored in a glass container with water to prevent desiccation. The conventional grid count method was used to measure leaf area ($n = 7$) on a 1-centimeter grid paper by counting grids covered by leaf multiplied by the area of a grid. The

Leaf Mass per Area (LMA) was then calculated as the leaf dry mass and leaf area ratio. Leaf dry mass was obtained by oven-drying the samples at 65°C for several days.

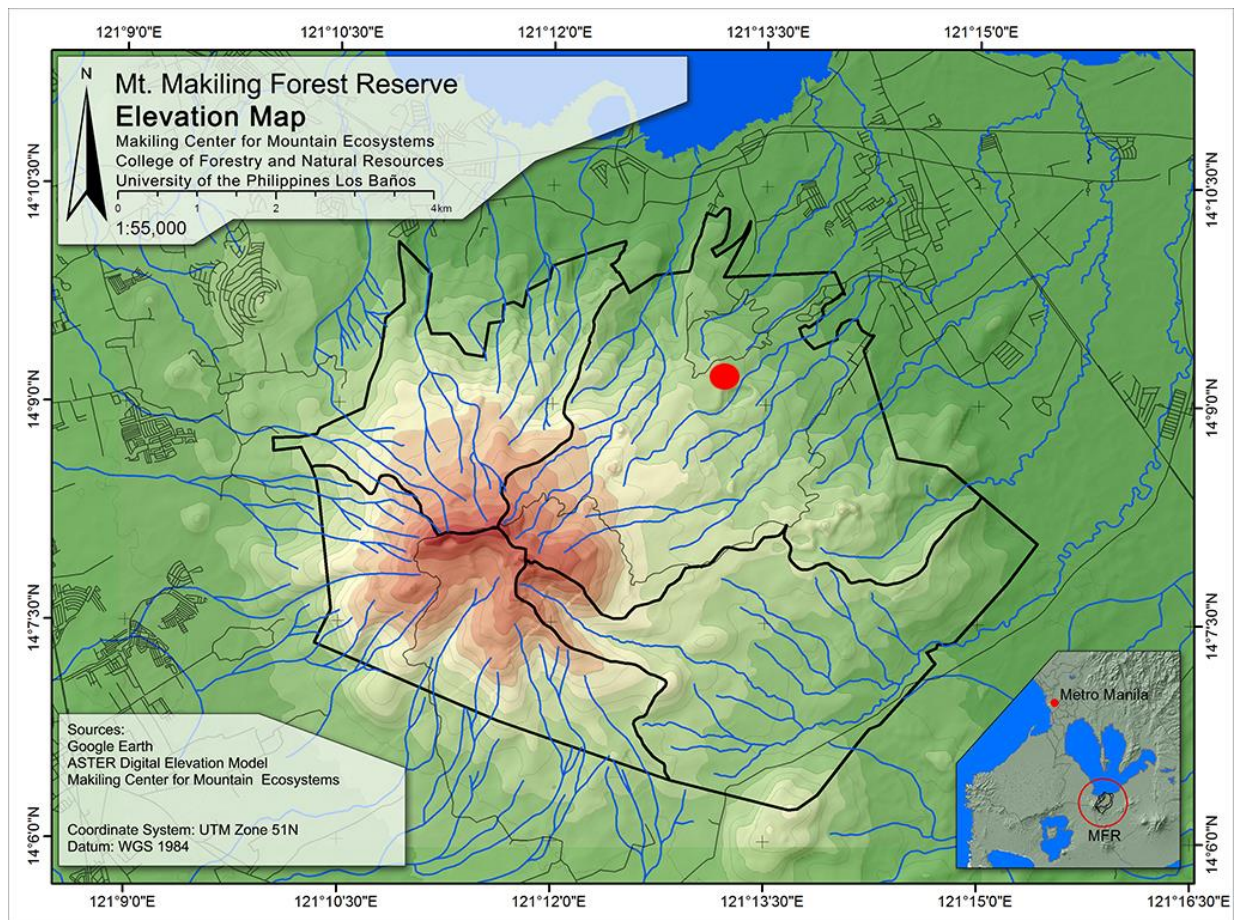


Fig. 1. Location of the study site (red dot) where shaded and sun-exposed seedlings of *B. Papyrifera* were selected. Source: Makiling Center for Mountain Ecosystems (MCME), <https://makiling.center/mt-makiling-maps/>.

A freehand technique was used to analyze young leaf, stem, and root anatomical structures of shaded and sun-exposed seedlings ($n = 7$) of *B. papyrifera*. A 1 mm × 1 mm leaf sample was collected from the mid-section of the leaf, taking into account the midrib and leaf blades. We specifically collected 1–2 mm long stem samples from the orthotropic branches of each shaded and sun-exposed seedling, located approximately 5 cm from the highest terminal bud. Only lateral roots, approximately 1–2 mm in diameter, were considered for this study. A sharp blade was used to cut very thin cross-sections ($n = 4$) of the leaf, stem, and roots, which were then stained with safranin solution (c.a. 5%). The staining process was carried out to easily determine the anatomical tissues in the cross-section under a compound light microscope at 40× magnification. The thickness (μm) of palisade and spongy mesophyll tissues, the thickness of xylem parenchyma cells, and the diameter of all xylem vessels in stem and roots were measured using the ImageJ processing software. Lastly, the stomatal density was determined following the leaf impression technique using transparent nail polish (Hernandez et al. 2022).

2.3. Measurement of Stomatal Conductance

Sun-exposed and shaded, healthy seedlings were randomly selected to measure stomatal conductance (g_s , $\text{mol m}^{-2}\text{s}^{-1}$) using a hand-held leaf porometer (SC-1, Meter Group, Inc., United States). Measurements were taken daily between 9:00 a.m. and 12:00 p.m. in the fully grown young leaves attached to a 5–6 node orthotropic branch of *B. papyrifera*.

2.4. Data and Statistical Analysis

The acquired data's normal distribution was assessed using the "Shapiro.test" tool in R statistical software (version R-3.5.1). A one-way ANOVA was used to examine the significant variations in the thickness of palisade and spongy mesophyll tissues, the thickness of xylem parenchyma cells, and the diameter of xylem vessels of both stem and root, and stomatal conductance between shaded and sun-exposed seedlings. All computations were done in R with a significance threshold of $\alpha = 0.05$.

3. Results and Discussion

The results found that the leaf area (LA) of *B. papyrifera* was larger in the sun-exposed than in the shaded condition (**Table 1**). This result indicates an adaptive response to sustain seedling-level energy capture to maximize the rate of photosynthesis, particularly in sun-exposed conditions. When seedlings of *B. papyrifera* experienced an open environment with a higher light intensity than those under the shaded area, there may have been an increased demand for allocating more energy and resources to photosynthesis. The seedlings may have changed their leaf growth pattern to meet the demand for efficient photosynthesis.

Table 1. Morphological traits of *B. papyrifera* in two different light conditions in Mount Makiling Forest Reserve

| Morphological traits | Light conditions | |
|---|---------------------------|---------------------------|
| | Shaded | Sun-exposed |
| Leaf area (cm) | 16.61(1.32) ^b | 21.19 (2.08) ^a |
| Leaf mass per area (g m^{-2}) | 0.12 (0.01) ^b | 0.15 (0.01) ^a |
| Stomata density (no. μm^{-2}) | 15.33 (1.13) ^a | 17.56 (1.12) ^a |

Notes: Values in parentheses are the standard deviations. Different lowercase letters indicate significant difference between shaded and sun-exposed conditions.

A previous study also reported similar results, i.e., shaded conditions had negative LA growth due to short leaf life span (Miyazawa et al. 2014). Other studies attributed the reduced LA of *B. papyrifera* in shaded conditions to shade intolerance and low carbon gains (Percy et al. 2005; Evans and Poorter 2001). Such a significant decrease in LA can also be ascribed to shade avoidance syndrome (SAS) of most shade-intolerant plants (Ciolfi et al. 2013). One of the SAS responses is increased leaf hyponasty (Tang et al. 2022), expressed in the reduction in leaf size of the shaded seedlings of *B. papyrifera*. SAS could weaken the plant's structure (Ballaré et al. 2017), which can be explained by the observed significant decline in LA in shaded seedlings. Several studies, however, found that smaller/thinner leaves generally have lower construction costs, leading to higher plant growth rates (Nagel and Griffin 2004; Griffin 1994; Funk 2013). Consequently, the result suggests leaf plasticity of the species in response to varying light

conditions, enabling them to thrive in heavily exposed areas, such as degraded or barren lands, where light intensity is generally high. It supports the higher leaf mass per area (LMA) observed in the sun-exposed than in the shaded condition. Sun leaves often have higher LMA than shade leaves, and such a characteristic enhances photosynthetic rates on an area basis (Choi et al. 2021). This result suggests that the seedlings are allocating more resources to producing denser and thicker leaves in response to increased light availability.

The LMA, the ratio between leaf dry mass and leaf area, is highly related to leaf processes, including leaf nitrogen concentration, photosynthesis, and respiration rates (Wright et al. 2004; John et al. 2017; Witkowski et al. 1991). It is also a good morphological trait widely used to indicate plant resistance to herbivory (de la Riva et al. 2016). This tendency explains the ability of the species to proliferate and spread easily in various environments and have high relative growth rates (RGR) as an invasive species, out-competing other slower-growing plants (Qureshi et al. 2020; Maan et al. 2021). Moreover, larger LA and LMA of sun-exposed seedlings than shaded seedlings may contribute to its overall large, dense canopy restricting understory growth (Bosu et al. 2013). It might be due to the larger values of these two leaf traits indicating an economic spectrum strategy regarding nutrient uptake and use, light capture, and carbon sequestration (Gara et al. 2021). Additionally, a positive correlation is usually observed between a species' capacity to have a larger LA and a higher relative RGR (Pepe et al. 2022).

Lastly, the stomatal density of *B. papyrifera* did not vary significantly between shaded and sun-exposed seedlings. The result can be attributed to the short-term duration of the experiment. Stomatal density may also adjust over long periods to suit the prevailing environmental conditions (Bertolino et al. 2019).

Results on morphological traits corresponded to the observed result on the anatomical traits of root, stem, and leaf of *B. papyrifera* (Fig. 2). Other invasive species (e.g., *Lantana camara* and *Chromolaena odorata*) also showed enhanced leaf anatomical traits such as thicker sclerenchyma and vascular tissues, which influenced photosynthetic assimilate transport (Rindyastuti et al. 2021). The study found that the spongy mesophyll is significantly thicker in sun-exposed seedlings than in shaded ones. It suggests that the total leaf thickness of sun-exposed seedlings is also significantly higher than shaded ones (Cioć and Pawłowska 2020). A previous study also reported a similar observation, i.e., spongy tissues-thickness significantly increased with increasing light intensity (Feng et al. 2019). Results can be attributed to the ability of the species to adapt to changing light conditions to optimize major physiological functions, such as photosynthesis and stomatal conductance. Leaves of some plants adjust their anatomical structure in response to prevailing light conditions, leading to increased photosynthetic efficiency (Hernandez et al. 2022; Evans and Poorter 2001; Théroux-Rancourt et al. 2023). It has also been reported that there is strong coordination between leaf anatomical traits in invasive and native species (Osunkoya et al. 2014). In this study, the stomatal conductance of sun-exposed seedlings of *B. papyrifera* was considerably higher than that in shaded seedlings (Fig. 3). A similar result was reported in an invasive *Berberis darwinii*, i.e., leaves of sun-exposed plants showed higher stomatal conductance than plants growing under the canopy and at the forest edge (Svriz et al. 2014). A thicker spongy mesophyll, which provides mechanical stability to the plant, is an important factor influencing gas exchange and other ion regulation in leaves (Karabourniotis et al. 2021). Thicker spongy mesophyll may have provided sun-exposed seedlings with a positive energy and carbon balance through efficient light capture, gas exchange, and water uptake and flow (Li et al. 2017).

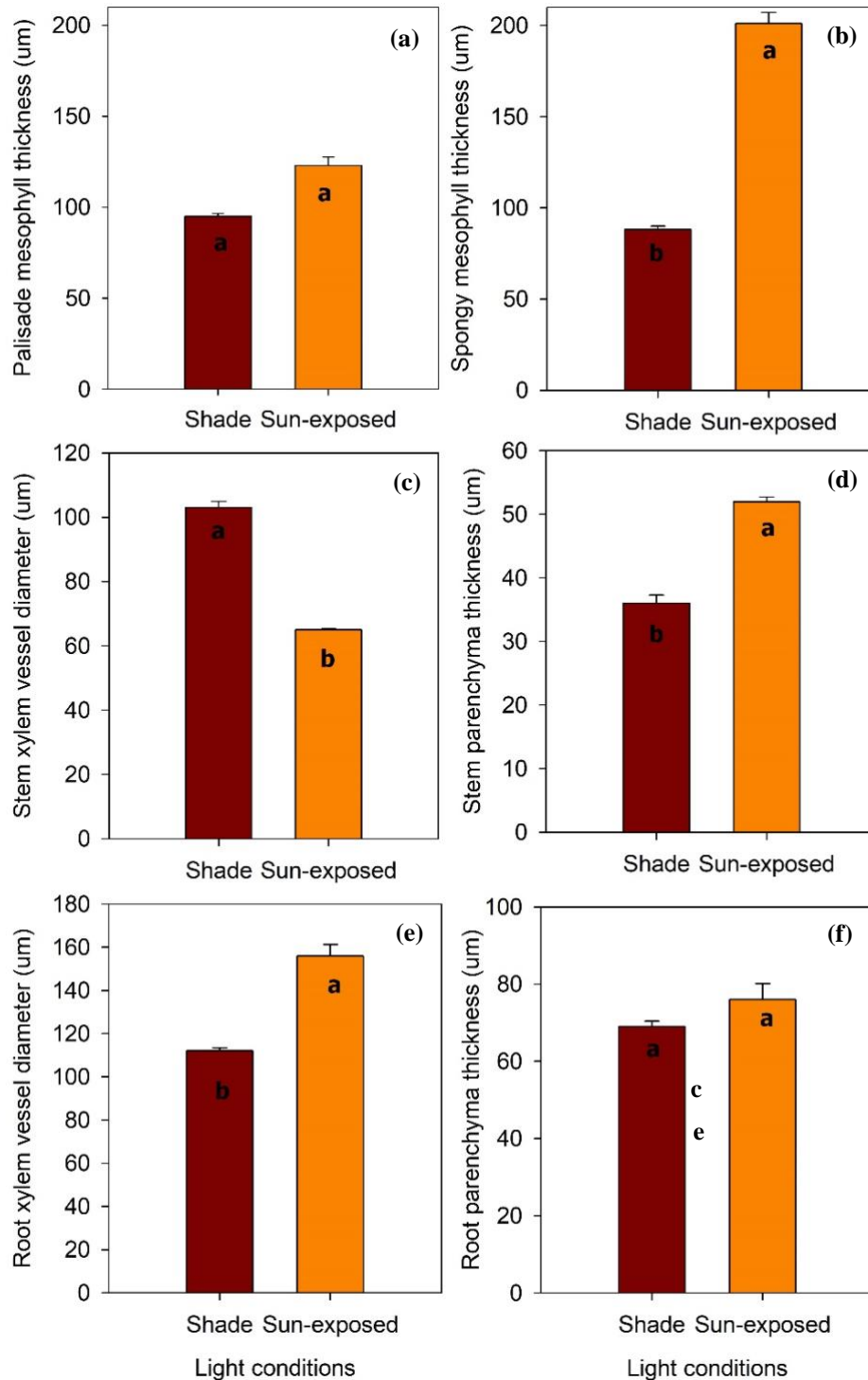


Fig. 2. The (a) palisade mesophyll thickness, (b) spongy mesophyll thickness, (c) stem xylem vessel diameter, (d) stem parenchyma thickness, (e) root xylem vessel diameter and (f) root parenchyma thickness of shaded and sun-exposed seedlings of *B. papyrifera*. Different lowercase letters indicate significant differences between light conditions.

The positive balance observed can be explained by the smaller diameter of xylem vessels but a greater thickness of xylem parenchyma cells (**Fig. 2** and **Fig. 4**). The combined effect of a smaller diameter of xylem vessels and a greater thickness of xylem parenchyma cells may have provided sun-exposed seedlings with more efficient water transport, nutrients, and water storage

and prevented seedlings from xylem embolism (Hernandez et al. 2022; He et al. 2023). It is because a smaller diameter of the xylem vessel can reduce water flow resistance, allowing for more efficient water and mineral transport from the roots to the other parts of a plant and preventing xylem damage (e.g., breakage, embolism). Because the primary function of the xylem is to carry large volumes of water and solutes, a continuous system of connecting tubes with a relatively low resistance to water flow is thought crucial (De Boer and Volkov 2003), especially in sun-exposed seedlings that were continuously photosynthesizing. Hence, thicker parenchyma cells in the stem cortex may have played a crucial role not only in the storage of water but also in starch produced during active photosynthesis. The thicker layer of parenchyma cells may have added strength to the vascular tissues to reduce the risk of collapse (Spicer 2014). Thus, this modification in the diameter of the xylem vessel and xylem parenchyma thickness with changing light conditions can further describe the invasiveness of *B. papyrifera*, as even a small change in the radius of xylem vessels will give a large change in resistance (De Boer and Volkov 2003).

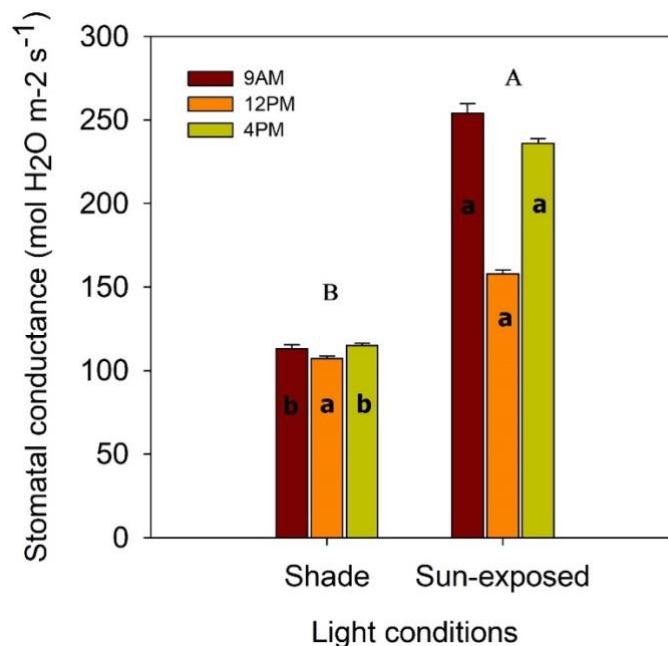


Fig. 3. Stomatal conductance of shaded and sun-exposed seedlings of *B. papyrifera*. Different uppercase and lowercase letters indicate significant differences between light conditions and time points, respectively.

A contrasting pattern was detected in the root xylem vessel diameter (**Fig. 2** and **Fig. 4**). Sun-exposed seedlings had higher root xylem vessel diameters than shaded seedlings. The result can be attributed to increased LA, spongy mesophyll thickness, and stem parenchyma thickness. Such increases may have enabled efficient photosynthesis, as shown indirectly by increased stomatal conductance, and resulted in increased cell division and growth, such as the development of wider root xylem vessels. This result corresponds to the decreased stem xylem vessel of sun-exposed seedlings. A study observed a continuous tapering pattern of vessels from roots to stems and branches, influencing hydraulic efficiency (Lübbe et al. 2021). The study of Shimizu et al. (2004) also partly supports our findings because they found significant increases in LA, LMA, and fine-root surface area during the shade-to-sun transfer experiment.

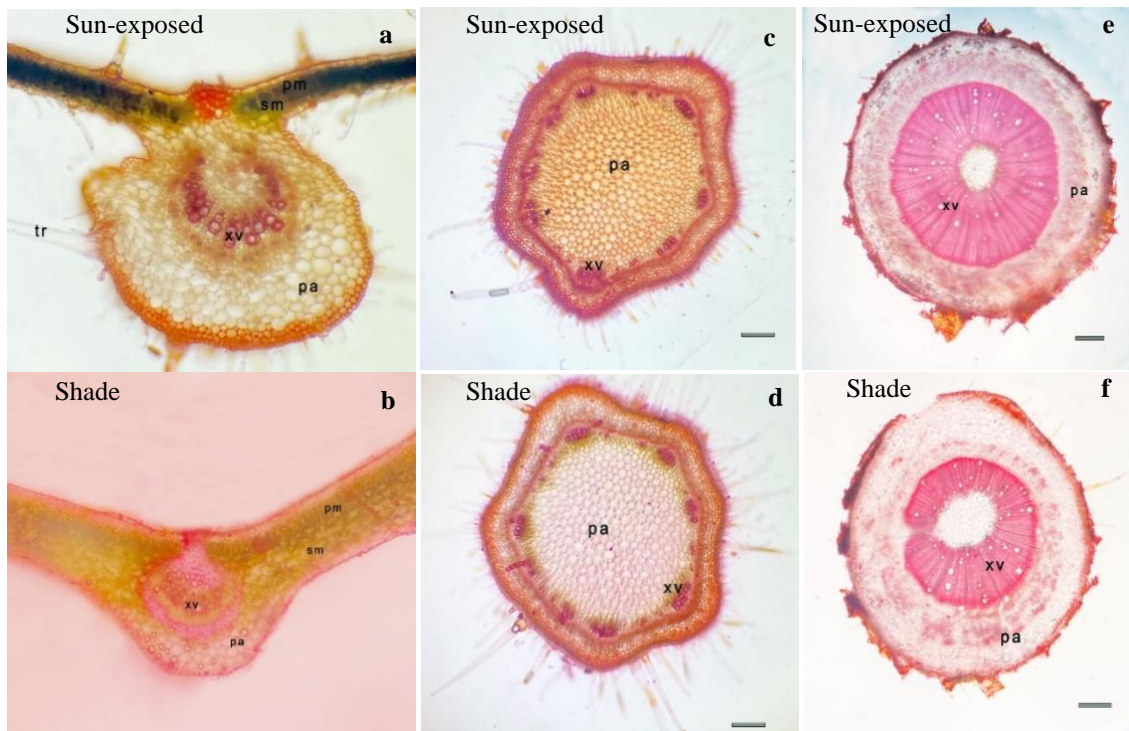


Fig. 4. Leaf (a-b), stem (c-d), and root (e-f) anatomical structures of shaded and sun-exposed seedlings of *B. papyrifera*. The scale bar represents 5 μ m. xy, pa, pm, and sm denote the xylem vessel, parenchyma, palisade mesophyll, and spongy mesophyll, respectively.

4. Conclusions

The present study revealed significant variations in leaf, stem, and root morphoanatomy, and stomatal conductance between shaded and sun-exposed seedlings of *B. papyrifera*. Sun-exposed seedlings exhibited larger LA, LMA, spongy mesophyll thickness, stem parenchyma thickness, and root xylem vessel diameter and reduced stem xylem vessel diameter, likely as an adaptive mechanism to enhance stomatal conductance in response to higher light exposure. The findings may provide valuable implications for managing or controlling invasiveness in highly exposed areas and maximizing the positive ecological benefits of *B. papyrifera*.

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References

- Ballaré, C. L., and Pierik, R. 2017. The Shade-Avoidance Syndrome: Multiple Signals and Ecological Consequences. *Plant, Cell and Environment* 40(11): 2530–2543. DOI: [10.1111/pce.12914](https://doi.org/10.1111/pce.12914)
- Barker, C. 2002. Plate 432. *Broussonetia papyrifera*. *Curtis's Botanical Magazine* 19: 8–18. DOI: [10.1111/1467-8748.00324](https://doi.org/10.1111/1467-8748.00324)

- Bertolino, L. T., Caine, R. S., and Gray, J. E. 2019. Impact of Stomatal Density and Morphology on Water-Use Efficiency in a Changing World. *Frontiers in Plant Science* 10: 225. DOI: [10.3389/fpls.2019.00225](https://doi.org/10.3389/fpls.2019.00225)
- Bosu, P. P., Apetorgbor, M. M., Nkrumah, E. E., and Bandoh, K. P. 2013. The Impact of *Broussonetia papyrifera* (L.) Vent. on Community Characteristics in the Forest and Forest-Savannah Transition Ecosystems of Ghana. *African Journal of Ecology* 51: 528–535. DOI: [10.1111/aje.12063](https://doi.org/10.1111/aje.12063)
- Brancalion, P. H. S., Campoe, O., Mendes, J. C. T., Noel, C., Moreira, G. G., Melis, J., and Guillemot, J. 2019. Intensive Silviculture Enhances Biomass Accumulation and Tree Diversity Recovery in Tropical Forest Restoration. *Ecological Applications* 29(2): e01847. DOI: [10.1002/eap.1847](https://doi.org/10.1002/eap.1847)
- Cavaleri, M. A., and Sack, L. 2010. Comparative Water Use of Native and Invasive Plants at Multiple Scales: A Global Meta-Analysis. *Ecology* 91(9): 2705–2715. DOI: [10.1890/09-0582.1](https://doi.org/10.1890/09-0582.1)
- Choi, D., Jang, W., Toda, H., and Yoshikawa, M. 2021. Differences in Characteristics of Photosynthesis and Nitrogen Utilization in Leaves of the Black Locust (*Robinia pseudoacacia* L.) According to Leaf Position. *Forests* 12(3): 348. DOI: [10.3390/f12030348](https://doi.org/10.3390/f12030348)
- Chung, K. F., Kuo, W. H., Hsu, Y. H., Li, Y. H., Rubite, R. R., and Xu, W. B. 2017. Molecular Recircumscription of *Broussonetia* (Moraceae) and the Identity and Taxonomic Status of *B. Kaempferi* var. *Australis*. *Botanical Studies* 58: 11. DOI: [10.1186/s40529-017-0165-y](https://doi.org/10.1186/s40529-017-0165-y)
- Cioć, M., and Pawłowska, B. 2020. Leaf Response to Different Light Spectrum Compositions During Micropropagation of *Gerbera axillary* Shoots. *Agronomy* 10(11): 1832. DOI: [10.3390/agronomy10111832](https://doi.org/10.3390/agronomy10111832)
- Ciolfi, A., Sessa, G., Sassi, M., Possenti, M., Salvucci, S., Carabelli, M., Morelli, G., and Ruberti, I. 2013. Dynamics of the Shade-Avoidance Response in *Arabidopsis*. *Plant Physiology* 163: 331–353. DOI: [10.1104/pp.113.221549](https://doi.org/10.1104/pp.113.221549)
- Čuda, J., Skálová, H., Janovský, Z., and Pyšek, P. 2013. Habitat Requirements, Short-Term Population Dynamics and Coexistence of Native and Invasive *Impatiens* Species: A Field Study. *Biological Invasions* 16(1): 177–190. DOI: [10.1007/s10530-013-0512-1](https://doi.org/10.1007/s10530-013-0512-1)
- Čuda, J., Skálová, H., Janovský, Z., and Pyšek, P. 2015. Competition Among Native and Invasive *Impatiens* Species: the Roles of Environmental Factors, Population Density and Life Stage. *AoB PLANTS* 7: plv033. DOI: [10.1093/aobpla/plv033](https://doi.org/10.1093/aobpla/plv033)
- D'Antonio, C. M., August-Schmidt, E., and Fernandez-Going, B. 2016. *Invasive Species and Restoration Challenges*. Island Press. Washington, DC. DOI: [10.5822/978-1-61091-698-1_8](https://doi.org/10.5822/978-1-61091-698-1_8)
- De Boer, A. H., and Volkov, V. 2003. Logistics of Water and Salt Transport Through the Plant: Structure and Functioning of the Xylem. *Plant, Cell and Environment* 26(1): 87–101. DOI: [10.1046/j.1365-3040.2003.00930.x](https://doi.org/10.1046/j.1365-3040.2003.00930.x)
- de la Riva, E. G., Olmo, M., Poorter, H., Ubera, J., and Villar, R. 2016. Leaf Mass per Area (LMA) and Its Relationship with Leaf Structure and Anatomy in 34 Mediterranean Woody Species along a Water Availability Gradient. *PLoS ONE* 11(2): e0148788. DOI: [10.1371/journal.pone.0148788](https://doi.org/10.1371/journal.pone.0148788)
- Evans, J. R., and Poorter, H. 2001. Photosynthetic Acclimation of Plants to Growth Irradiance: the Relative Importance of Specific Leaf Area and Nitrogen Partitioning in Maximizing Carbon Gain. *Plant Cell Environment* 24: 755–767. DOI: [10.1046/j.1365-3040.2001.00724.x](https://doi.org/10.1046/j.1365-3040.2001.00724.x)

- Feng, L., Raza, M. A., Li, Z., Chen, Y., Khalid, M. H., Du, J., Liu, W., Wu, X., Song, C., Yu, L., Zhang, Z., Yuan, S., Yang, W., and Yang, F. 2019. The Influence of Light Intensity and Leaf Movement on Photosynthesis Characteristics and Carbon Balance of Soybean. *Frontiers in Plant Science* 9: 1952. DOI: [10.3389/fpls.2018.01952](https://doi.org/10.3389/fpls.2018.01952)
- Finch, D. M., Butler, J. L., Runyon, J. B., Fetting, C. J., Kilkenny, F. F., Jose, S., Frankel, S. J., Cushman, S. A., Cobb, R. C., Dukes, J. S., Hicke, J. A., and Amelon, S. K. 2021. Effects of Climate Change on Invasive Species. *Springer eBooks* (pp. 57–83). DOI: [10.1007/978-3-030-45367-1_4](https://doi.org/10.1007/978-3-030-45367-1_4)
- Funk, J. L. 2013. The Physiology of Invasive Plants in Low-Resource Environments. *Conservation Physiology* 1(1): cot026. DOI: [10.1093/conphys/cot026](https://doi.org/10.1093/conphys/cot026)
- Gara, T. W., Rahimzadeh-Bajgiran, P., and Darvishzadeh, R. 2021. Forest Leaf Mass per Area (LMA) through the Eye of Optical Remote Sensing: A Review and Future Outlook. *Remote Sensing* 13(17): 3352. DOI: [10.3390/rs13173352](https://doi.org/10.3390/rs13173352)
- Griffin, K. L. 1994. Calorimetric Estimates of Construction Cost and Their Use in Ecological Studies. *Functional Ecology* 8(5): 551. DOI: [10.2307/2389915](https://doi.org/10.2307/2389915)
- Handayani, A., Zuhud, E. A., and Junaedi, D. I. 2023. Naturalized Alien Plant as Traditional Medicine Resources: A Study from Cibodas Biosphere Reserve, West Java. *Jurnal Sylva Lestari* 11(2): 298–319. DOI: [10.23960/jysl.v11i2.715](https://doi.org/10.23960/jysl.v11i2.715)
- He, L., Fu, Y., Liu, Z., and Wei, P. 2023. Structural Variation Patterns in Xylem Vessels and Parenchyma Cells and Their Association with Tree Evolution. *Forests* 14(5): 950. DOI: [10.3390/f14050950](https://doi.org/10.3390/f14050950)
- Hernandez, J. O., and Park, B. B. 2022. The Leaf Trichome, Venation, and Mesophyll Structural Traits Play Important Roles in the Physiological Responses of Oak Seedlings to Water-Deficit Stress. *International Journal of Molecular Sciences* 23(15): 8640. DOI: [10.3390/ijms23158640](https://doi.org/10.3390/ijms23158640)
- Ilyas, M., Shah, S., Lai, Y. W., Sher, J., Bai, T., Zaman, F., Bibi, F., Koul, M., Wani, S. H., Majrashi, A., Alharby, H. F., Hakeem, K. R., Wang, Y. J., and Rather, S. A. 2022. Leaf Functional Traits of Invasive Grasses Conferring High-Cadmium Adaptation Over Natives. *Frontiers in Plant Science* 13: 869072. DOI: [10.3389/fpls.2022.869072](https://doi.org/10.3389/fpls.2022.869072)
- John, G. P., Scoffoni, C., Buckley, T. N., Villar, R., Poorter, H., and Sack, L. 2017. The Anatomical and Compositional Basis of Leaf Mass per Area. *Ecology Letters* 20(4): 412–425. DOI: [10.1111/ele.12739](https://doi.org/10.1111/ele.12739)
- Karabourniotis, G., Liakopoulos, G., Bresta, P., and Nikolopoulos, D. 2021. The Optical Properties of Leaf Structural Elements and Their Contribution to Photosynthetic Performance and Photoprotection. *Plants* 10(7): 1455. DOI: [10.3390/plants10071455](https://doi.org/10.3390/plants10071455)
- Kaushik, P., Pati, P. K., Khan, M. L., and Khare, P. K. 2022. Plant Functional Traits Best Explain Invasive Species' Performance within a Dynamic Ecosystem - A Review. *Trees, Forests and People* 8: 100260. DOI: [10.1016/j.tfp.2022.100260](https://doi.org/10.1016/j.tfp.2022.100260)
- Li, L., Ma, Z., Niinemets, Ü., and Guo, D. 2017. Three Key Sub-Leaf Modules and the Diversity of Leaf Designs. *Frontiers in Plant Science* 8: 1542. DOI: [10.3389/fpls.2017.01542](https://doi.org/10.3389/fpls.2017.01542)
- Lübbe, T., Lamarque, L. J., Delzon, S., Torres Ruiz, J. M., Burlett, R., Leuschner, C., and Schuldt, B. 2021. High Variation in Hydraulic Efficiency but Not Xylem Safety Between Roots and Branches in Four Temperate Broad-Leaved Tree Species. *Functional Ecology* 36(3): 699–712. DOI: [10.1111/1365-2435.13975](https://doi.org/10.1111/1365-2435.13975)

- Maan, I., Kaur, A., Singh, H. P., Batish, D. R., and Kohli, R. K. 2021 Exotic Avenue Plantations Turning Foe: Invasive Potential, Distribution and Impact of *Broussonetia papyrifera* in Chandigarh, India. *Urban Forestry and Urban Greening* 59: 127010. DOI: [10.1016/j.ufug.2021.127010](https://doi.org/10.1016/j.ufug.2021.127010)
- Marwat, K. B., Hashim, S., and Ali, H. 2010. Weed Management: A Case Study from North-West Pakistan. *Pakistan Journal of Botany* 42: 341–353.
- Miyazawa, Y., Manythong, C., Fukuda, S., and Ogata, K. 2014. Comparison of the Growth Traits of a Commercial Pioneer Tree Species, Paper Mulberry (*Broussonetia papyrifera* L. Vent.), with Those of Shade-Tolerant Tree Species: Investigation of the Ecophysiological Mechanisms Underlying Shade-Intolerance. *Agroforestry Systems* 88(5): 907–919. DOI: [10.1007/s10457-014-9735-0](https://doi.org/10.1007/s10457-014-9735-0)
- Nagel, J. M., and Griffin, K. L. 2004. Can Gas-Exchange Characteristics Help Explain the Invasive Success of *Lythrum salicaria*? *Biological Invasions* 6(1): 101–111. DOI: [10.1023/b:binv.0000010125.93370.32](https://doi.org/10.1023/b:binv.0000010125.93370.32)
- Osunkoya, O. O., Boyne, R., and Scharaschkin, T. 2014. Coordination and Plasticity in Leaf Anatomical Traits of Invasive and Native Vine Species. *American Journal of Botany* 101(9): 1423–1436. DOI: [10.3732/ajb.1400125](https://doi.org/10.3732/ajb.1400125)
- Pandey, V. C. 2012. Invasive Species Based Efficient Green Technology for Phytoremediation of Fly Ash Deposits. *Journal of Geochemical Exploration* 123: 13–18. DOI: [10.1016/j.gexplo.2012.05.008](https://doi.org/10.1016/j.gexplo.2012.05.008)
- Pearcy, R. W., Valladares, F., Wright, S. J., and de Paulis, E. L. 2004. A Functional Analysis of the Crown Architecture of Tropical Forest Psychotria Species: Do Species Vary in Light Capture Efficiency and Consequently in Carbon Gain and Growth? *Oecologia* 139: 163–177. DOI: [10.1007/s00442-004-1496-4](https://doi.org/10.1007/s00442-004-1496-4)
- Pearson, D. E., Ortega, Y. K., Eren, Ö., and Hierro, J. L. 2018. Community Assembly Theory as a Framework for Biological Invasions. *Trends in Ecology and Evolution* 33(5): 313–325. DOI: [10.1016/j.tree.2018.03.002](https://doi.org/10.1016/j.tree.2018.03.002)
- Pepe, M., Gratani, L., Crescente, M. F., Puglielli, G., and Varone, L. 2022. Daily Temperature Effect on Seedling Growth Dynamic of Three Invasive Alien Species. *Frontiers in Plant Science* 13: 837449. DOI: [10.3389/fpls.2022.837449](https://doi.org/10.3389/fpls.2022.837449)
- Pötzelsberger, E., Lapin, K., Brundu, G., Adriaens, T., Andonovski, V., Andrašev, S., Bastien, J. C., Brus, R., Čurović, M., Čurović, Ž., Cvjetković, B., Đodan, M., Domingo-Santos, J. M., Gazda, A., Henin, J. M., Hernea, C., Karlsson, B., Keča, L., Keren, S., and Hasenauer, H. 2020. Mapping the Patchy Legislative Landscape of Non-Native Tree Species in Europe. *Forestry: An International Journal of Forest Research* 93(4): 567–586. DOI: [10.1093/forestry/cpaa009](https://doi.org/10.1093/forestry/cpaa009)
- Pyšek, P., and Richardson, D. M. 2010. Invasive Species, Environmental Change and Management, and Health. *Annual Review of Environment and Resources* 35(1): 25–55. DOI: [10.1146/annurev-environ-033009-095548](https://doi.org/10.1146/annurev-environ-033009-095548)
- Qureshi, H., Anwar, T., Fatima, S., Akhtar, S., Khan, S., Waseem, M., Mohibullah, M., Shirani, M., Riaz, S., and Azeem, M. 2020. Invasion Impact Analysis of *Broussonetia papyrifera* in Pakistan. *Polish Journal of Environmental Studies* 29(4): 2825–2831. DOI: [10.15244/pjoes/111320](https://doi.org/10.15244/pjoes/111320)

- Rindyastuti, R., Hapsari, L., and Byun, C. 2021. Comparison of Ecophysiological and Leaf Anatomical Traits of Native and Invasive Plant Species. *Journal of Ecology and Environment* 45: 4. DOI: [10.1186/s41610-020-00174-7](https://doi.org/10.1186/s41610-020-00174-7)
- Roy, H. E., Bacher, S., Essl, F., Adriaens, T., Aldridge, D. C., Bishop, J. D., Blackburn, T. M., Branquart, E., Brodie, J., Carboneras, C., Cottier-Cook, E. J., Copp, G. H., Dean, H. J., Eilenberg, J., Gallardo, B., Garcia, M., García-Berthou, E., Genovesi, P., Hulme, P. E., and Rabitsch, W. 2018. Developing a List of Invasive Alien Species Likely to Threaten Biodiversity and Ecosystems in the European Union. *Global Change Biology* 25(3): 1032–1048. DOI: [10.1111/gcb.14527](https://doi.org/10.1111/gcb.14527)
- Scheepens, J. F., Frei, E. S., and Stöcklin, J. 2010. Genotypic and Environmental Variation in Specific Leaf Area in a Widespread Alpine Plant after Transplantation to Different Altitudes. *Oecologia* 164(1): 141–150. DOI: [10.1007/s00442-010-1650-0](https://doi.org/10.1007/s00442-010-1650-0)
- Seelenfreund, D., Clarke, A., Oyanedel, N., Piña, R., Lobos, S., Matisoo-Smith, E., and Seelenfreund, A. 2010. Paper Mulberry (*Broussonetia papyrifera*) as a Commensal Model for Human Mobility in Oceania: Anthropological, Botanical and Genetic Considerations. *New Zealand Journal of Botany* 48(3–4): 231–247. DOI: [10.1080/0028825x.2010.520323](https://doi.org/10.1080/0028825x.2010.520323)
- Shimizu, M., Ishida, A., and Hogetsu, T. 2004. Root Hydraulic Conductivity and Whole-Plant Water Balance in Tropical Saplings Following a Shade-to-Sun Transfer. *Oecologia* 143(2): 189–197. DOI: [10.1007/s00442-004-1797-7](https://doi.org/10.1007/s00442-004-1797-7)
- Silvertown, J., and Charlesworth, D. 2009. *Introduction to Plant Population Biology*. John Wiley and Sons Ltd. Chichester.
- Spicer, R. 2014. Symplasmic Networks in Secondary Vascular Tissues: Parenchyma Distribution and Activity Supporting Long-Distance Transport. *Journal of Experimental Botany* 65(7): 1829–1848. DOI: [10.1093/jxb/ert459](https://doi.org/10.1093/jxb/ert459)
- Svriz, M., Damascos, M. A., Lediuk, K. D., Varela, S. A., and Barthélémy, D. 2014. Effect of Light on the Growth and Photosynthesis of an Invasive Shrub in its Native Range. *AoB PLANTS* 6: plu033. DOI: [10.1093/aobpla/plu033](https://doi.org/10.1093/aobpla/plu033)
- Tang, W., Guo, H., Baskin, C. C., Xiong, W., Yang, C., Li, Z., Song, H., Wang, T., Yin, J., Wu, X., Miao, F., Zhong, S., Tao, Q., Zhao, Y., and Sun, J. 2022. Effect of Light Intensity on Morphology, Photosynthesis and Carbon Metabolism of Alfalfa (*Medicago sativa*) Seedlings. *Plants* 11(13): 1688. DOI: [10.3390/plants11131688](https://doi.org/10.3390/plants11131688)
- Théroux-Rancourt, G., Herrera, J. C., Voggeneder, K., De Bernardinis, F., Luijken, N., Nocker, L., Savi, T., Scheffknecht, S., Schneck, M., and Tholen, D. 2023. Analyzing Anatomy Over Three Dimensions Unpacks the Differences in Mesophyll Diffusive Area between Sun and Shade *Vitis vinifera* Leaves. *AoB PLANTS* 15(2): plad001. DOI: [10.1093/aobpla/plad001](https://doi.org/10.1093/aobpla/plad001)
- Venette, R. C., Gordon, D. R., Juzwik, J., Koch, F. H., Liebhold, A. M., Peterson, R. K., Sing, S. E., and Yemshanov, D. 2021. Early Intervention Strategies for Invasive Species Management: Connections between Risk Assessment, Prevention Efforts, Eradication, and Other Rapid Responses. *Invasive Species in Forests and Rangelands of the United States* 111–131. DOI: [10.1007/978-3-030-45367-1_6](https://doi.org/10.1007/978-3-030-45367-1_6)
- Wang, C., Liu, J., Xiao, H., and Zhou, J. 2016. Differences in Leaf Functional Traits between *Rhus typhina* and Native Species. *CLEAN – Soil, Air, Water* 44(11): 1591–1597. DOI: [10.1002/clean.201600144](https://doi.org/10.1002/clean.201600144)
- Walther, G. R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta Dukát, Z., and Bugmann, H. 2009. Alien Species in a Warmer World: Risks and

- Opportunities. *Trends in Ecology and Evolution* 24(12): 686–693. DOI: [10.1016/j.tree.2009.06.008](https://doi.org/10.1016/j.tree.2009.06.008)
- Weidlich, E. W., Flórido, F. G., Sorrini, T. B., and Brancalion, P. H. 2020. Controlling Invasive Plant Species in Ecological Restoration: A Global Review. *Journal of Applied Ecology* 57(9): 1806–1817. DOI: [10.1111/1365-2664.13656](https://doi.org/10.1111/1365-2664.13656)
- Witkowski, E. T. F., and Lamont, B. B. 1991. Leaf Specific Mass Confounds Leaf Density and Thickness. *Oecologia* 88: 486–493. DOI: [10.1007/bf00317710](https://doi.org/10.1007/bf00317710)
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., and Villar, R. 2004. The Worldwide Leaf Economics Spectrum. *Nature* 428(6985): 821–827. DOI: [10.1038/nature02403](https://doi.org/10.1038/nature02403)
- Xiao, F., Chen, C., Gong, W., Xiong, Y., Zhou, Y., Guo, W., Li, B., and Wang, Y. 2022. Trade-Off Between Shade Tolerance and Chemical Resistance of Invasive *Phytolacca americana* under Different Light Levels Compared with Its Native and Exotic Non-Invasive Congeners. *Environmental and Experimental Botany* 196: 104809. DOI: [10.1016/j.envexpbot.2022.104809](https://doi.org/10.1016/j.envexpbot.2022.104809)