Flora 271 (2020) 151680

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Comparisons of irradiance utilization efficiency by invasive *Chromolaena odorata* and its three co-occurring species in one planted understory

Xiong Shi[a,b], Gang Liu[c], Yu-Long Zheng[a,b,d,*]

[a] CAS key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, 666303, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] College of Life Sciences, Shanxi Normal University, Xi'an, Shannxi, 710119, China
[d] Center of Conservation Biology, Core Botanical Gardens, Chinese Academy of Sciences, Menglun, Mengla 666303, Yunnan, China

ARTICLE INFO

Keywords:
Biological invasion
Chromolaena odorata
Irradiance utilization efficiency
Net photosynthetic rate
Leaf anatomy

ABSTRACT

High irradiance utilization efficiency is one important character for some invasive plants. *Chromolaena odorata* is one noxious invasive species originating from Latin America, which had spread widely in most tropical and subtropical areas. To explore why *C. odorata* perform better than native plants in the understory of planted forests, we compared the irradiance utilization efficiency between invasive *C. odorata* and three co-occurring species (*Merremia vitifolia, Pueraria phaseoloides,* and *Litsea monopetala*). We found that *C. odorata* had lower leaf thickness but higher specific leaf area, net photosynthetic rate per leaf thickness and photosynthetic nitrogen use efficiency than the three native species. The photosynthetic resistance to irradiance damage was stronger for *C. odorata* than for the three native species. These traits may have contributed to the higher performance of *C. odorata* than native plants, which may in turn facilitate its invasion in the understory.

1. Introduction

Invasive alien plants have caused a series of problems, which not only destroy the biodiversity and integrity of natural ecosystems, but also threaten the human health (D'Antonio and Kark, 2002; Schaffner et al., 2020). Identifying the mechanisms that contribute to the success of invasive plants is crucial for controlling them. Numerous studies have elucidated high resource utilization efficiency of the invasive plant is an important factor for its successful invasion (Pattison et al., 1998; Zheng et al., 2012). Valliere (2019) found invasive species had higher water use efficiency (WUE) than native species. Several studies had shown photosynthetic nitrogen use efficiency (PNUE) was also higher for invasive species than native species (Feng et al., 2008a; Zheng et al., 2009).

Irradiance is an important resource for plants, which influences both vegetative and reproductive growth (Feng et al., 2007; Poorter, 2001). The ability for plants to capture and utilize irradiance is an important determinant of growth potential and fitness, especially in irradiance limited environments (Feng et al., 2007). Several studies have proposed that in similar environment conditions, irradiance utilization efficiency was higher for invasive plants than for native plants (Zheng et al., 2012). Some functional traits are strongly related with irradiance use efficiency (Valladares et al., 2000). Normally, higher specific leaf area (SLA) indicates the plant has lower leaf construction cost, faster growth rate and higher photosynthetic nitrogen use efficiency (PNUE) (Perez-Harguindeguy et al., 2013). For instance, Smith and Knapp (2001) found that invasive plants have higher SLA compared with native plants. In addition, Riveron-Giro et al. (2017) discovered characteristic of leaf anatomy was also related with irradiance use efficiency, and contributed to successful invasion of exotic plants.

The measurement of chlorophyll fluorescence is another effective method to assess irradiance utilization efficiency. For instance, photosynthetic efficiency of PSII (Phi 2) represents the true photosynthetic rate, and non-photo-chemical quenching (NPQ) indicates the resistance for high irradiance damage of the plant (Kuhlgert et al., 2016). Under high irradiance condition, excess absorbed irradiance energy could induce a huge decrease in PSII activity, and cause photoinhibition (Takahashi and Badger, 2011), especially in shade plants (Barth et al., 2001; Kitao et al., 2000). The result of Yamashita et al. (2000) indicated that invasive plants possessed high irradiance acclimation capacity based on this method. However, the comparison of chlorophyll fluorescence characters between invasive and native species is still rare in field condition. Meanwhile, only few studies compared the irradiance utilization between invasive and native plants in the understory of

---

[*] Corresponding author.
E-mail addresses: Zhengyulong980@126.com, Zhengyl@xtbg.org.cn (Y.-L. Zheng).

https://doi.org/10.1016/j.flora.2020.151680
Received 1 June 2020; Received in revised form 10 August 2020; Accepted 11 August 2020

planted forests.

Chromolaena odorata (L.) King & Robinson (Asteraceae) is a perennial shrub originating in Central and Southern America, and it has become a globally noxious invader in tropical and subtropical areas (Qin et al., 2013). It usually forms monoculture in introduced ranges, and severely threatens agriculture, biodiversity and ecosystem function (Goodall and Erasmus, 1996; Zheng et al., 2015).

Understory of the planted forest (UPF) is one of susceptible areas for *C. odorata* (Goodall and Erasmus, 1996). We postulate that the invader may possess higher irradiance utilization efficiency than native plants in the UPF. In this study, we compared the irradiance use efficiency of *C. odorata* with its three co-occurring plants under the understory of one planted forest. The efficiency is evaluated by the combination of functional traits, chlorophyll fluorescence and leaf anatomy results. We aim to explore whether *C. odorata* has higher irradiance utilization efficiency than native plants in the understory of one planted forest.

2. Materials and methods

2.1. Study site and species

This study was conducted at Xishuangbanna Tropical Botanical Garden (21°56’N, 101°15’E, 560 m a.s.l.) of the Chinese Academy of Science (XTBG-CAS), which is located in Menglun, Mengla, Yunnan Province, China. The mean annual temperature is 21.7 °C; the mean temperature of the hottest month (July) is 25.3 °C, and the mean temperature of coolest month (January) is 15.6 °C. The average annual precipitation is 1557 mm, with a dry period lasting from November to April (Zheng et al., 2015).

The experimental site was one planted forest dominated by *Chukrasia tabularis, Melia toosendan* and *Gmelina arborea*, which is near from scientific research center of XTBG-CAS. The understory of this forest is seriously invaded by *C. odorata*, and its coverage is over 60%. *Merremia vitifolia, Pueraria phaseoloides*, and *Litsea monopetala* were three native plants, they are common in this understory, and all seedlings of them co-occur with *C. odorata. Merremia vitifolia* is a perennial twining or prostrate plant of the Convolvulaceae family. *Pueraria phaseoloides* is a perennial herbaceous vine of the Fabaceae family. *Litsea monopetala* is an evergreen tree of Lauraceae.

2.2. Leaf anatomy

In March 2019, at 9:30 to 11:30 am, fully expanded and well-developed leaves of six individual seedlings per species were collected and put into sealing pockets, which were quickly brought back to the laboratory. The leaves of *C. odorata, M. vitifolia, P. phaseoloides* and *L. monopetala* were collected from some individuals in the understory of above planted forest. These individuals grew naturally in this understory of planted forest, and all of them were at seedling stage. Each selected individual was at least 1 m apart with other individuals. The height of *C. odorata* was about 1m, and *P. phaseoloides* and *L. monopetala*’s were 0.2-0.4 m, as for *M. vitifolia*, which is difficult to measure due to the twining property. There are five steps in the anatomy experiment of epidermis. Firstly, the leaf was cut into 3-4 small segments near to midrib in a bottle, and then we added potassium chlorate, nitrite acid solution, distilled water, respectively. Secondly, after one night, we washed the leaf segment with distilled water, and then conserved them in the centrifuge tube with glycerol. Then, we took and washed it again with potassium hydroxide solution, the mesophyll would be removed by dissecting needle. Fourthly, it would be used to make the permanent slide after saturation with aceto-carmine stain. Finally, the slide was observed by binocular optical microscope DM2000 (Leica, Germany) and photographed, the width and length of epidermis were calculated by ImageJ software (Schneider et al., 2012) using with 40×microscopic objectives, and epidermis density (epidermis number per view) was 20×microscopic objectives. In addition, hand-cut transverse sections were taken from the region near to midrib, observed by binocular optical microscope DM2000 (Leica, Germany) and photographed, the thickness of palisade mesophyll were measured by ImageJ software using with 20×microscopic objectives. In addition, 6 views were selected on each leaf when above indexes measuring or observing.

2.3. Measurements of chlorophyll fluorescence and functional traits

In March 2019, fluorescence measurement was conducted by MultispeQ-Beta device (PhotosynQ, USA) at 10:00 (optimal irradiance, intensity is about 500 μmol m^{-2} s^{-1}) and 14:00 (high irradiance, 1000 μmol m^{-2} s^{-1}) respectively. Following parameters were measured according to the method of Kuhlgert et al. (2016): photosynthetic efficiency of PSII (Phi 2, true photosynthetic rate), photosynthetic non photo-chemical quenching (NPQ), relative chlorophyll and leaf thickness. Measurements were carried out on the new fully expanded leaves. For each species, 11 individual seedlings were selected as replicates.

In addition, as mentioned above, the net photosynthetic rate (*Pn*) of 5 individual seedlings per species were measured with Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA) at saturated light intensity (800 μmol m^{-2} s^{-1}) and 380 μmol mol^{-1} CO_2 concentration. The leaf area of each individual was measured with Li-3000A leaf area meter (Li-Cor, Lincoln, NE, USA). Then the leaves were oven-dried for 48 h at 80 ℃ and weighted. The specific leaf area (SLA) was calculated as leaf area / leaf dry mass.

2.4. Statistical analyses

One-way ANOVAs (Tukey’s test) were used to test for the difference among species at the same irradiance, and for each species. Multiple comparison was tested with Duncan, and homogeneity of variances was tested with Levene Statistic. Independent-samples t test was used to compare the difference of each parameter between 10:00 and 14:00. All analyses were carried out by SPSS 18.0 (SPSS Inc. Chicago, Illinois, USA).

3. Results

Firstly, palisade mesophyll thickness of invasive *C. odorata* was significantly lower than *M. vitifolia* but higher than *L. monopetala* and *P. phaseoloides* (Fig. 1A), while palisade / leaf thickness and *Pn* / palisade thickness of *C. odorata* were significantly higher than three native species (Fig. 1B, C). The size of epidermal cell of *C. odorata* was smaller than *L. monopetala* and *M. vitifolia*, but the epidermal density was highest (Fig. 2).

The invader’s relative chlorophyll increased significantly from morning to noon (Fig. 3A), and the change in PhiNPQ of the invader was significantly greater than *M. vitifolia* and *P. phaseoloides* (Fig. 3B). Phi2 was not significantly different between the invader and three co-occurring species (Fig. 4A), but the invader had higher *Pn* (net photosynthetic rate) than *L. monopetala* and *P. phaseoloides* (Fig. 4B). Moreover, *C. odorata* showed significantly lower leaf thickness and higher SLA (Fig. 5).

4. Discussion

Some studies clarified that palisade mesophyll could facilitate CO_2 diffusion and intensify the light penetration capability (Evans, 1999; Mendes et al., 2001). Although palisade mesophyll thickness of *C. odorata* is at middle compared with three native species, its ratio of palisade / leaf thickness and *Pn* / palisade thickness were all significantly highest (Fig. 1), suggesting that these may be two mechanisms to maintain greater photosynthetic performance for *C. Odorata* through palisade regulation. First, it could allocate more resources for palisade building, which ensure the higher proportion, which ensured the higher proportion of palisade in leaf structure. In addition, its palisade structure

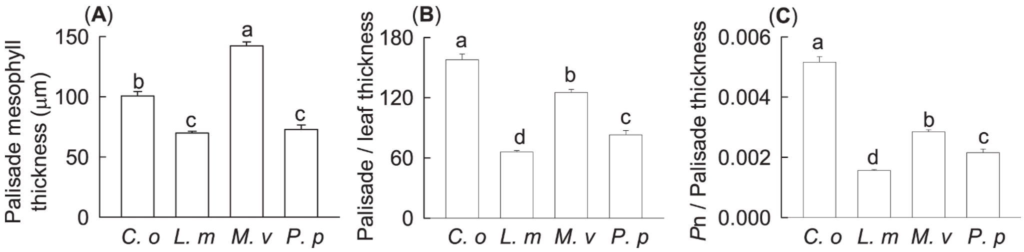

Fig. 1. (A) Palisade mesophyll thickness, (B) palisade / leaf thickness and (C) *Pn* / palisade thickness of *C. odorata* (*C. o*) and native *L. monopetala* (*L. m*), *M. vitifolia* (*M. v*), and *P. phaseoloides* (*P. p*). Mean ± SE are given; different lowercase letters indicate significant difference among species.

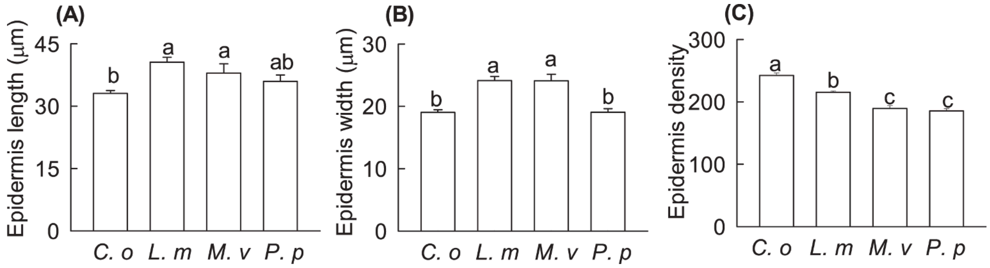

Fig. 2. (A) Epidermis length, (B) epidermis width and (C) epidermis density of *C. odorata* (*C. o*) and native *L. monopetala* (*L. m*), *M. vitifolia* (*M. v*), and *P. phaseoloides* (*P. p*). Mean ± SE are given. Different lowercase letters indicate significant difference among species.

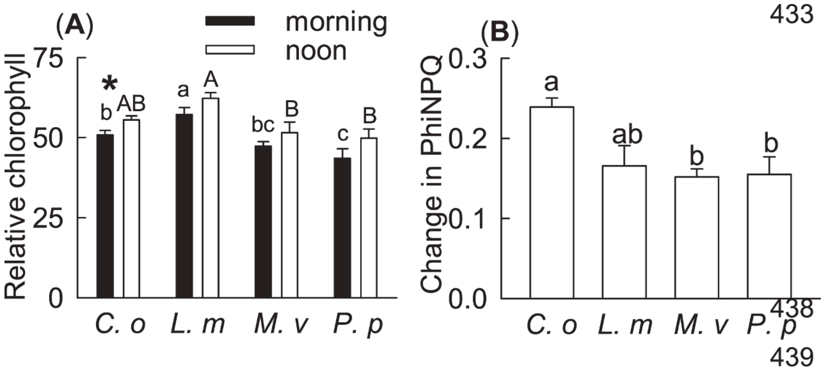

Fig. 3. (A) Relative chlorophyll and (B) change in PhiNPQ of *C. odorata* (*C. o*) and native *L. monopetala* (*L. m*), *M. vitifolia* (*M. v*), and *P. phaseoloides* (*P. p*). Mean ± SE. In (A), different lowercase letters indicate significant difference among species in morning (low irradiance), different capital letters indicate significant difference among species at noon (high irradiance), and the asterisk indicates significant difference between morning and noon for the same species. In (B), different lowercase letters indicate significant difference among species.

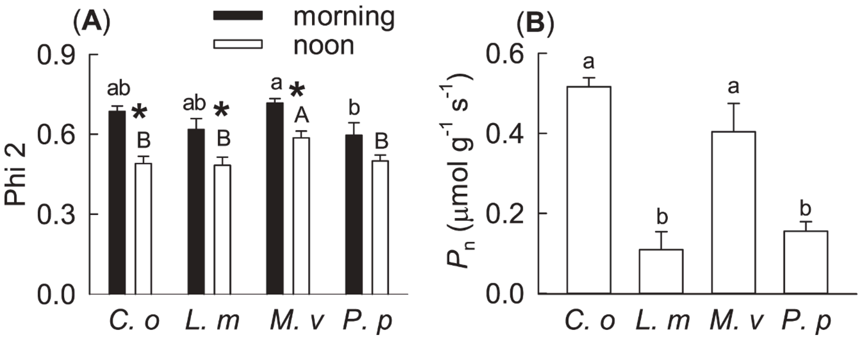

Fig. 4. (A) Phi2 and (B) *Pn* of *C. odorata* (*C. o*), and native *L. monopetala* (*L. m*), *M. vitifolia* (*M. v*), and *P. phaseoloides* (*P. p*). Mean ± SE. In (A), different lowercase letters indicate significant difference among species in morning (low irradiance), different capital letters indicate significant difference among species at noon (high irradiance), and the asterisk indicates significant difference between morning and noon for the same species. In (B), different lowercase letters indicate significant difference among species.

may be adjusted to capture more irradiance and increase carbon fixation, and thus, to account for higher *Pn* per palisade thickness (Vogelmann et al., 1996).

Bosabalidis and Kofidis (2002) found that small epidermal cells with high density could prevent cells from rupturing due to lack of water under acidic, saline and high temperature conditions. In irradiance stress environment, the highest epidermal density and smaller epidermal cell size (than *L. monopetala* and *M. vitifolia*) could prevent water transpiration, then give advantage to *C. odorata* (Fig. 2).

Chlorophyll is a major determinant of photosynthetic process, which absorbed and transferred the irradiance energy to chemical energy. Chlorophyll could also reveal the leaf nitrogen status due to its positive correlation with leaf nitrogen content (Xiong et al., 2015). What was striking was that relative chlorophyll of *C. odorata* changed significantly from morning to noon (Fig. 3A), which might due to its seedlings were at a period of rapid growth. Another reason may be related with the

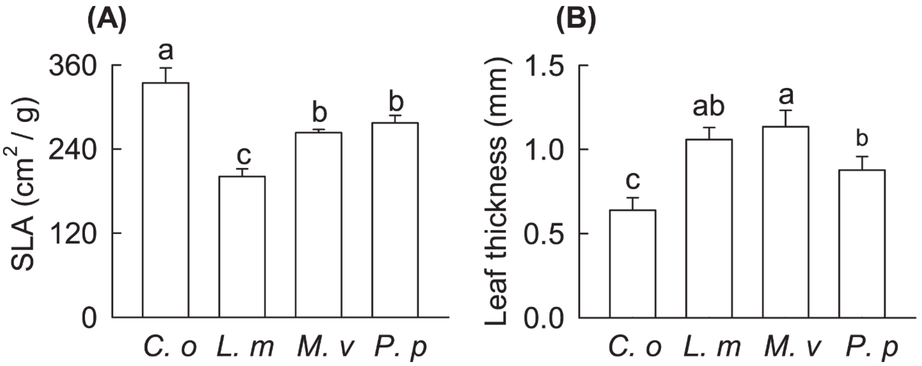

Fig. 5. (A) Specific leaf area (SLA) and (B) leaf thickness of *C. odorata* (*C. o*) and native *L. monopetala* (*L. m*), *M. vitifolia* (*M. v*), and *P. phaseoloides* (*P. p*). Mean±SE, different lowercase letters indicate significant difference among species.

increase of leaf nitrogen content for the invader. Some previous studies revealed that invasive species have higher nitrogen absorbing capacity (Hu et al., 2019), and others have shown that invasive plants invest more nitrogen in photosynthesis to fulfill rapid growth (Feng et al., 2009; Sardans et al., 2017). Thus, we could conclude that *C. odorata* possessed two characters above. High irradiance at noon usually induces photoinhibition (Taiz and Zeiger, 2002), especially for plants grown in understory (Krause et al., 2012). PhiNPQ is an index for photosynthetic protection, which reflects the ability of plant dissipates excess irradiance energy through non-photochemical quenching (Kuhlgert et al., 2016). The greater change of PhiNPQ for the invader indicated that *C. odorata* could balance and utilize excess energy more effectively than *M. vitifolia* and *P. phaseoloides* (Fig. 3B). Similar results were also found by Song et al. (2010) in invasive *Wedelia trilobata*. As for woody plants, it's essential to possess the effective photoprotection mechanism for *L. monopetala*.

Compared with *L. monopetala* and *P. phaseoloides, Pn* was higher for *C. odorata* while Phi2 was not significantly different (Fig. 4), which indicates its higher accumulation of carbohydrate and less respiration cost, which could contribute to the rapid growth rate of *C. odorata* (Liao et al., 2007; Zheng et al., 2012). Leishman et al. (2010) also found that some invasive plants had a lower respiration rate for a given *Pn* than native species. With respect to *M. vitifolia*, the highest Phi2 at noon may contribute to its similar *Pn* with *C. odorata*, which would also ensure its rapid growth (Fig. 4).

Invasive *C. odorata* had significantly higher SLA but lower leaf thickness than its co-occurring natives (Fig. 5). Feng et al. (2008b) found SLA relates to leaf construction cost, photosynthesis and PNUE. Based on this, we inferred that *C. odorata* might have lower leaf construction cost and higher PNUE than natives. Leaf thickness also plays a key role in the process of photosynthesis, in general, thicker leaves are occurred in sunnier habitat and indicate lower CO_2 diffusion (Perez-Harguindeguy et al., 2013). Thus, the thinner leaves of *C. odorata* facilitate the photosynthesis through increasement of CO_2 diffusion. The above two traits indicated that *C. odorata* could capture more light than natives through decreasing leaf thickness and expanding leaf area in the understory.

Wright et al. (2004) found that quick return species' leaves were usually characterized by high SLA and *Pn*, and more minerals. The hypothesis of the evolution of nitrogen allocation was proposed to explain alien plant invasion, which posit that invasive plants invest more nitrogen on photosynthetic apparatus and thus to facilitate rapid growth rate (Sardans et al., 2017). In this study, the higher *Pn*, relative chlorophyll changing, the palisade construction, thinner leaves and higher SLA, all of these traits revealed that the economic leaf construction of invasive *C. odorata*, which further facilitate its higher irradiance utilization efficiency and PNUE. Thus, the invader could grow rapidly through more available irradiance energy to capture and utilize in the understory.

5. Conclusions

The higher *Pn* per leaf thickness, *Pn* per palisade thickness of invasive *C. odorata* facilitated its accumulation of carbohydrate and fast growth, suggesting its higher irradiance utilization efficiency. Lower leaf thickness and higher SLA contributed to its lower leaf construction cost, and the greater change in relative chlorophyll related with its higher PNUE. In addition, small epidermal size of *C. odorata* could prevent water loss during gas exchanging. The invader was also more resistant to irradiance damage due to its greater change in PhiNPQ. Overall, these traits contribute higher irradiance utilization efficiency of *C. odorata*, which may relate with its invasiveness in the understory of planted forest.

Credit author statement

X.S. and Y.L.Z. designed the research. X.S and Y.L.Z performed the research. G. L. gave some suggestion for this paper. X.S. and Y.L.Z. wrote and revised the paper.

Declaration of Competing Interest

This manuscript has not been published or presented elsewhere in entirety or in part and is not under consideration by another journal. We have read and understood your journal's policies, and we believe that neither the manuscript nor the study violates any of these. There are no conflicts of interest to declare.

Acknowledgement

We are grateful to Zuo Lina and Tao Shuangfeng for collecting some data. This study was funded by the National Natural Science Foundation of China (31670546, 31870524), and the CAS 135 program (2017XTBG-F01).

References

Barth, C., Krause, G.H., Winter, K., 2001. Responses of photosystem I compared with photosystem II to high-light stress in tropical shade and sun leaves. Plant Cell Environ. 24, 163–176.
Bosabalidis, A.M., Kofidis, G., 2002. Comparative effects of drought stress on leaf anatomy of two olive cultivars. Plant Sci. 163, 375–379.
D'Antonio, C.M., Kark, S., 2002. Impacts and extent of biotic invasions in terrestrial ecosystems. Trends Ecol. Evol. 17, 202–204.
Evans, J.R., 1999. Leaf anatomy enables more equal access to light and CO_2 between chloroplasts. New Phytol 143, 93–104.
Feng, Y.L., 2008a. Nitrogen allocation and partitioning in invasive and native *Eupatorium* species. Physiol. Plant. 132, 350–358.
Feng, Y.L., Fu, G.L., Zheng, Y.L., 2008b. Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners. Planta 228, 383–390.
Feng, Y.L., Lei, Y.B., Wang, R.F., Callaway, R.M., Valiente-Banuet, A., Inderjit, Li, Y.P., Zheng, Y.L., 2009. Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an invasive plant. Proc. Natl. Acad. Sci. U. S. A. 106, 1853–1856.

Feng, Y.L., Wang, J.F., Sang, W.G., 2007. Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. Acta Oecol. 31, 40–47.

Goodall, J.M., Erasmus, D.J., 1996. Review of the status and integrated controlof the invasivealien weed, *Chromolaena odorata*, in South Africa. Agric. Ecosyst. Environ. 56, 151–164.

Hu, C.C., Lei, Y.B., Tan, Y.H., Sun, X.C., Xu, H., Liu, C.Q., Liu, X.Y., 2019. Plant nitrogen and phosphorus utilization under invasive pressure in a montane ecosystem of tropical China. J. Ecol. 107, 372–386.

Kitao, M., Lei, T.T., Ko.ike, T., Tobita, H., Maruyama, Y., 2000. Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. Plant Cell Environ. 23, 81–89.

Krause, G.H., Winter, K., Matsubara, S., Krause, B., Jahns, P., Virgo, A., Aranda, J., Garcia, M., 2012. Photosynthesis, photoprotection, and growth of shade-tolerant tropical tree seedlings under full sunlight. Photosynthesis Res. 113, 273–285.

Kuhlgert, S., Austic, G., Zegarac, R., Osei-Bonsu, I., Hoh, D., Chilvers, M.I., Roth, M.G., Bi, K., TerAvest, D., Weebadde, P., Kramer, D.M., 2016. MultispeQ Beta: a tool for large-scale plant phenotyping connected to the open PhotosynQ network. Roy. Soc. Open Sci. 3, 17.

Leishman, M.R., Thomson, V.P., Cooke, J., 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. J. Ecol. 98, 28–42.

Liao, C.Z., Luo, Y.Q., Jiang, L.F., Zhou, X.H., Wu, X.W., Fang, C.M., Chen, J.K., Li, B., 2007. Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. Ecosystems 10, 1351–1361.

Mendes, M.M., Gazarini, L.C., Rodrigues, M.L., 2001. Acclimation of Myrtus communis to contrasting Mediterranean light environments — effects on structure and chemical composition of foliage and plant water relations. Environ. Exp. Bot. 45, 165–178.

Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117, 449–459.

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quetier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234.

Poorter, L., 2001. Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. Funct. Ecol. 15, 113–123.

Qin, R.M., Zheng, Y.L., Valiente-Banuet, A., Callaway, R.M., Barclay, G.F., Pereyra, C.S., Feng, Y.L., 2013. The evolution of increased competitive ability, innate competitive advantages, and novel biochemical weapons act in concert for a tropical invader. New Phytol. 197, 979–988.

Riveron-Giro, F.B., Damon, A., Garcia-Gonzalez, A., Solis-Montero, L., Aguilar-Romero, O., Ramirez-Marcial, N., Nieto, G., 2017. Anatomy of the invasive orchid *Oeceoclades maculata*: ecological implications. Bot. J. Linn. Soc. 184, 94–112.

Sardans, J., Bartrons, M., Margalef, O., Gargallo-Garriga, A., Janssens, I.A., Ciais, P., Obersteiner, M., Sigurdsson, B.D., Chen, H.Y.H., Penuelas, J., 2017. Plant invasion is associated with higher plant-soil nutrient concentrations innutrient-poor environments. Glob. Change Biol. 23, 1282–1291.

Schaffner, U., Steinbach, S., Sun, Y., Skjoth, C.A., de Weger, L.A., Lommen, S.T., Augustinus, B.A., Bonini, M., Karrer, G., Sikoparija, B., Thibaudon, M., Muller-Scharer, H., 2020. Biological weed control to relieve millions from Ambrosia allergies in Europe. Nat. Commun. 11, 7.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.

Smith, M.D., Knapp, A.K., 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. Int. J. Plant Sci. 162, 785–792.

Song, L.Y., Chow, W.S., Sun, L.L., Li, C.H., Peng, C.L., 2010. Acclimation of photosystem II to high temperature in two *Wedelia* species from different geographical origins: implications for biological invasions upon global warming. J. Exp. Bot. 61, 4087–4096.

Taiz, L., Zeiger, E., 2002. Plant Physiology, third ed. Sinauer Associates, Sunderland.

Takahashi, S., Badger, M.R., 2011. Photoprotection in plants: a new light on photosystem II damage. Trends Plant Sci. 16, 53–60.

Valladares, F., Martinez-Ferri, E., Balaguer, L., Perez-Corona, E., Manrique, E., 2000. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytol. 148, 79–91.

Valliere, J.M., 2019. Tradeoffs between growth rate and water-use efficiency in seedlings of native perennials but not invasive annuals. Plant Ecol. 220, 361–369.

Vogelmann, T.C., Nishio, J.N., Smith, W.K., 1996. Leaves and light capture: light propagation and gradients of carbon fixation within leaves. Trends Plant Sci. 1, 65–70.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.

Xiong, D.L., Chen, J., Yu, T.T., Gao, W.L., Ling, X.X., Li, Y., Peng, S.B., Huang, J.L., 2015. SPAD-based leaf nitrogen estimation is impacted by environmental factors and crop leaf characteristics. Sci. Rep. 5, 12.

Yamashita, N., Ishida, A., Kushima, H., Tanaka, N., 2000. Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. Oecologia 125, 412–419.

Zheng, Y.L., Feng, Y.L., Liu, W.X., Liao, Z.Y., 2009. Growth, biomass allocation, morphology, and photosynthesis of invasive *Eupatorium adenophorum* and its native congeners grown at four irradiances. Plant Ecol. 203, 263–271.

Zheng, Y.L., Feng, Y.L., Lei, Y.B., Liao, Z.Y., 2012. Comparisons of plastic responses to irradiance and physiological traits by invasive *Eupatorium adenophorum* and its native congeners. J. Plant Physio. 169, 884–891.

Zheng, Y.L., Feng, Y.L., Zhang, L.K., Callaway, R.M., Valiente-Banuet, A., Luo, D.Q., Liao, Z.Y., Lei, Y.B., Barclay, G.F., Silva-Pereyra, C., 2015. Integrating novel chemical weapons and evolutionarily increased competitive ability in success of a tropical invader. New Phytol. 205, 1350–1359.