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Photosynthesis in Co-occurring Invasive *Acacia* spp. and Native Bornean Heath Forest Trees at the Post-establishment Invasion Stage

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ABSTRACT

Seedlings of invasive species often exhibit superior physiological traits that facilitate their spread at early stages of invasion, although it is unclear whether these traits persist at the post-establishment stage. To determine whether mature exotic *Acacia* spp. possess superior traits over mature native plants, we compared foliar gas exchange and chlorophyll a fluorescence of *Acacia auriculiformis* and *Acacia mangium* coexisting with tropical heath forest tree species *Buchanania arborescens* and *Dillenia suffruticosa* in Brunei Darussalam. The CO₂ assimilation rates of *Acacia* spp. were significantly higher than those of heath species at current prevailing conditions of ~400 ppm ambient CO₂, 1,500 μmol m⁻² s⁻¹ photosynthetically active radiation and 30°C leaf temperature. The photosystem II of *Acacia* spp. exhibited significantly higher maximum quantum yield of primary photochemistry at comparable temperatures, and was more sensitive to an elevated temperature (42°C for 1 h). Better photosynthetic performance of *Acacia* spp., due to larger stomatal openings, better light harvesting efficiency, and greater plasticity in photosystem II, may enable adult *Acacia* trees to sustain a competitive growth advantage and suppress native tropical heath forest species. The competitive advantage maintained by *Acacia* spp. in post-establishment stage likely facilitates the establishment of monospecific *Acacia* stands in invaded heath forests.

KEYWORDS

Competitive advantage; heat stress; kerangas; OJIP test

Introduction

Exotic plants typically possess novel traits or extreme trait values, which confer competitive advantages over native species (Grotkopp, Rejmánek, & Rost, 2002; Matzek, 2012; Van Kleunen, Weber, & Fischer, 2010b). For example, Vitousek and Walker (1989) reported that N₂-fixing ability of the introduced *Myrica faya* facilitated its ability to out-compete the dominant native *Metrosideros polymorpha* and invade successfully into young volcanic sites in Hawaii, USA. Thus, comparisons of the performance of invasive alien species and co-occurring native plants have provided some insights into mechanisms of invasion success (Daehler, 2003; Funk, 2013; Hulme & Bernard-Verdier, 2017; Van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010a). The contribution of specific traits and trait values that define successful invaders varies according to different invasion

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stages, i.e., transport, introduction, establishment, and spread (Andersen, Adams, Hope, & Powell, 2004; Blackburn et al., 2011; Dawson, Burslem, & Hulme, 2009; Van Kleunen, Dawson, & Maurel, 2015).

About 300 Australian *Acacia* spp. have been introduced globally, primarily for forestry and horticulture (Lowe, Browne, Boudjelas, & De Poorter, 2000; Morris, Esler, Barger, Jacobs, & Cramer, 2011). Of these, 23 species have become highly invasive and cause negative impacts on ecosystem services of invaded areas (Richardson & Rejmánek, 2011). Australian *Acacia* spp. were introduced into Brunei Darussalam, Northwest Borneo in the early 1990s for land rehabilitation and plantation forestry, and have since spread into many natural habitats, especially disturbed tropical heath forests (Osunkoya, Othman, & Kahar, 2005). Bornean heath forests (Kerangas) are lowland tropical forests on nutrient-poor sandy soils but still maintain moderately high levels of plant endemism (Din, Metali, & Sukri, 2015) and productivity (Miyamoto, Kohyama, Rahajoe, Mirmanto, & Simbolon, 2016; Miyamoto, Rahajoe, Kohyama, & Mirmanto, 2007; Wong, Ahmad, Low, & Kalat, 2015). Intact Bornean heath forests are diminishing at an alarming rate (MacKinnon, Hatta, Halim, & Mangalik, 1997; Miyamoto et al., 2007) and some well-preserved Kerangas patches in Brunei are facing numerous negative impacts from anthropogenic activities such as land-use changes and fire (Din et al., 2015). Populations of *Acacia* spp. have been previously reported spreading into Brunei's heath forests (Osunkoya & Damit, 2005), with documented negative effects on Kerangas soils (Matali & Metali, 2015) and soil seed bank compositions (Suhaili, Tennakoon, & Sukri, 2015). The invasion of *Acacia* spp. usually reduces species richness of invaded ranges to ultimately establish monospecific *Acacia* spp. stands (Lazzaro et al., 2014). However, some native tree species such as *Buchanania arborescens*, *Calophyllum inophyllum*, *Dillenia suffruticosa*, *Melastoma beccarianum*, and *Ploiarium alternifolium* can still co-exist with mature exotic *Acacia* spp. in disturbed Bornean heath forest patches (Tuah, 2014).

Seedlings of *A. mangium* were reported as having faster growth than those of a common Bornean heath species, *Melastoma beccarianum*, only under high-light, but not low-light, conditions (Osunkoya et al., 2005). This suggests that high-light conditions may facilitate the photosynthetic activities of *Acacia* spp., thereby conferring *Acacia* spp. seedlings a competitive advantage over native heath species seedlings under tropical conditions. However, whether adult invasive *Acacia* spp. trees still sustain this superior photosynthetic performance compared to co-existing native heath species is still unclear.

Plant photosynthesis is mainly limited by stomatal conductance, the activation of ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (RuBisCO) and the electron transport capacity for RuBP regeneration (Farquhar & Sharkey, 1982; Hikosaka, Noguchi, & Terashima, 2016). Photosynthesis is also affected by light absorption of photosystems (PS) in the photosynthetic apparatus (Golbeck & Est, 2014). Additionally, photosynthetic traits in higher plants are strongly influenced by environmental variables such as soil and climate (Maire et al., 2015). Gas exchange measurements provide insights into instantaneous photosynthetic parameters, such as the CO₂ assimilation rate, stomatal conductance and transpiration rate, and insights into biochemical parameters of leaf photosynthesis, such as RuBisCO activity and electron transport capacity (Von Caemmerer & Farquhar, 1981). The analysis of chlorophyll *a* (Chl *a*) fluorescence transients provides information regarding the behavior of PS II, reflecting the structure, conformation, and function of the photosynthetic apparatus at any physiological state, such as under heat stress (Strasser, Srivastava, & Tsimilli-Michael, 2000).

Invasive plants typically exhibit leaf traits such as higher photosynthetic capacity per dry mass and lower leaf construction costs that promote rapid growth (Leishman, Haslehurst, Ares, & Baruch, 2007), often placing them differently along the leaf economics spectrum compared to native species (Wright et al., 2004), especially in sites with high resource availability (Leishman, Thomson, & Cooke, 2010; Penuelas et al., 2010). Most studies comparing invasive and native species have focused on characteristics of seedlings in the introduction and establishment stages (Grotkopp et al., 2002; Osunkoya et al., 2005) but information on adult plant invaders remains scarce (Muñoz, Linares, Castro-Díez, & Sass-Klaassen, 2015). In this study, we investigated whether invasive *Acacia* spp. maintain a competitive advantage in photosynthesis over native plant species at the post-establishment stage of invasion. We compared photosynthetic performances, i.e., foliar gas exchange and Chl *a* fluorescence, of adult trees of two invasive *Acacia* spp. [*Acacia auriculiformis* A. Cunn. ex Benth. and *A. mangium* Willd. (Leguminosae, Mimosoideae)] and two co-occurring native tree species [*Buchanania arborescens* (Blume) Blume (Anacardiaceae) and *Dillenia suffruticosa* (Griff.) Martelli (Dilleniaceae)] in a tropical heath forest patch in Brunei Darussalam. The two native species were selected as both species are commonly observed coexisting with *Acacia*-invaded heath forest patches in Brunei Darussalam (Tuah, 2014). We hypothesized that the adult trees of *A. auriculiformis* and *A. mangium* would exhibit higher photosynthetic rates compared to trees of the two native plant species, *Buchanania arborescens* and *Dillenia suffruticosa*.

Materials and methods

Study site and sampling procedures

This study was carried out in a coastal heath forest patch surrounding Universiti Brunei Darussalam campus (N 04 96.4' E 114 86.9', elevation of 43 m a.s.l.). Heath forests soils are podzolized sandy soils with low nutrient content and high acidity (Jaafar, Sukri, & Proches, 2016; Matali & Metali, 2015). The climate of Brunei Darussalam is aseasonal, with a mean monthly temperature of 28.2°C and total annual rainfall of 2182.2 mm recorded at the Brunei International Airport (ca. 2 km away from the study site) in 2016 (Brunei Darussalam Meteorological Department, unpublished data). *Acacia mangium* and *A. auriculiformis* are the two most dominant invasive *Acacia* spp. in Brunei Darussalam's coastal heath forests (Osunkoya & Damit, 2005), while both *B. arborescens* and *D. suffruticosa* are common in disturbed heath forests and in secondary forest sites in Borneo (Coode, Kirkup, Dransfield, Forman, & Said, 1996; Nakagawa et al., 2013; Rosleine & Suzuki, 2012).

Individual trees of the target species, with approximate heights between 6.0 and 7.0 m, were selected for sampling. The minimum distance between the two nearest individuals was ~10 m. Fully expanded and healthy mature phyllodes for *Acacia* spp. or leaves for heath forest species in the upper tree canopy from 6 (n = 6 for gas exchange measurements) and 30 (n = 30 for chlorophyll fluorescence measurements) individuals of each species were selected, and three phyllodes or leaves per individual were measured to obtain average values.

Gas exchange and chlorophyll *a* fluorescence transient measurements

The gas exchange of phyllodes or leaves was measured with a portable gas exchange system (LI-6400XT; Li-Cor, Lincoln, NE, USA), following Le, Tennakoon, Metali, Lim,

and Bolin (2016a, 2016b). The flow rate of the gas into the chamber, leaf temperature, photosynthetically active radiation (PAR), and relative humidity inside the chamber were maintained at $500 \mu\text{mol s}^{-1}$, 30°C , $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 60–65%, respectively. The air CO_2 concentration (C_a) in the chamber was varied at 50, 100, 150, 250, 400, 500, 700, 950, and 1,250 ppm to generate CO_2 photosynthetic response curves. The intercellular CO_2 concentration (C_i ; ppm), CO_2 assimilation rates (A ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s ; $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) and transpiration rate (E ; $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) were recorded directly from the output readings of the portable gas exchange system. The water use efficiency (WUE; $\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$) was calculated using the A/E ratio (Farquhar & Richards, 1984). The CO_2 response curves were generated by plotting A to varying C_a ($A-C_a$ curve) or C_i ($A-C_i$ curve).

The maximum carboxylation rate of RuBisCO (V_{cmax} ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), potential electron transport rate for regeneration of RuBP (J_{max} ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), RuBP-saturated CO_2 assimilation rate (A_c ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and RuBP-limited CO_2 assimilation rate (A_j ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) were generated by fitting $A-C_i$ curves into the Von Caemmerer–Berry biochemical model of photosynthesis (Farquhar, von Caemmerer, & Berry, 1980; Von Caemmerer, 2000) using the “plantecophys” package in R software (Duursma, 2015).

Chlorophyll fluorescence was induced by a red light at $3,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a saturation width at 1.0 sec (Strasser et al., 2000) and subsequently measured with a portable chlorophyll fluorometer (OS-30P+; Opti-science, Inc., Hudson, NH, USA). Detached phyllodes and leaves were dark-adapted and temperature-treated (25°C , 30°C , or 42°C) for 1 h, and Chl a fluorescence was recorded immediately after treatments as described by Yu and Ong (2002). Fluorescence intensities after light excitation at different time points (F_t), 20 μs (O), 3 ms (J) and 30 ms (I), and the maximal fluorescence (P) of each measurement were expressed after normalization to respective fluorescence intensities at 0 s (F_0). The Chl a fluorescence transient curves were generated by plotting normalized F_t versus time (ms, logarithmic scale). The quantum yields of Chl a at time zero were interpreted as: (i) the maximum quantum yield of primary photochemistry (ϕ_{P_0}), (ii) the quantum yield of electron transport (ϕ_{E_0}), (iii) the quantum yield of energy dissipation (ϕ_{D_0}), and (iv) the probability that a trapped exciton moves an electron into the electron transport beyond the primary quinone acceptor of PSII (ψ_0), as described by Strasser et al. (2000) and Strasser, Srivastava, and Tsimilli-Michael (2004).

Statistical analysis

Statistical tests were conducted with R version 3.2.3 (R Core Team, 2015). Data were first visualized using the ggqqplot function of “ggpubr” R package (Kassambara, 2017) and then statistically tested for normality using Shapiro test. One-way ANOVA and *post-hoc* Tukey’s tests were used to determine pairwise differences among investigated species in photosynthetic parameters at maximum (V_{cmax} and J_{max}), photosynthetic parameters measured at 400 ppm ambient CO_2 (A_c , A_j/A_c , A , g_s , E , WUE), Chl a fluorescence parameters (ϕ_{P_0} , ϕ_{E_0} , Ψ_0 and ϕ_{D_0}) and variation of photosynthetic parameters (A , g_s , E , WUE) induced by CO_2 elevation (from 400 to 500 ppm). A t -test was used to determine differences in Chl a fluorescence parameters (ϕ_{P_0} , ϕ_{E_0} , Ψ_0 , and ϕ_{D_0}) of the same species when subjected to different temperature treatments (30°C and 40°C).

Results

Gas exchange in *Acacia* spp. and native species

There was no difference in patterns of CO₂ response curves (A-C_a and A-C_i) between species from the same group, i.e. *Acacia* spp. or native species (Figure 1a & 1b). However, in comparison to native species, *Acacia* spp. tended to have higher A measured at the same comparable C_a in the range of 250–500 ppm (Figure 1a) but similar A measured at the same comparable C_i which is smaller than 350 ppm (Figure 1b). At the same comparable C_a greater than 950 ppm or C_i greater than 400 ppm, *Acacia* spp. showed lower A than native species (Figure 1a & 1b).

There were no significant differences in V_{cmax}, J_{max}, and A_c between species from the same group, i.e. *Acacia* spp. or native species (Table 1). There was no distinct difference in V_{cmax} between two groups, i.e. *Acacia* spp. vs. native species, but *Acacia* spp. exhibited a significantly lower J_{max} and A_j/A_c ratio than the native species ($P < 0.001$).

At C_a of 400 ppm, there were no significant differences in observed and fitted A, g_s, E, and WUE between species from the same group but *Acacia* spp. exhibited significantly higher A, g_s and E, and a significantly lower WUE than the native species ($P < 0.001$, Table 2). In response to the C_a elevation (from 400 to 500 ppm), *Acacia* spp. showed significantly smaller increases in A and significantly greater decreases in g_s and E ($P < 0.001$) when compared with the native species (Figure 2).

Chlorophyll *a* fluorescence of *Acacia* spp. and native species

Acacia spp. and native species exhibited different patterns of Chl *a* fluorescence transient curves in response to different temperature treatments (25°C, 30°C, and 42°C, Figure 3). *Acacia* spp. tended to exhibit lower relative maximal fluorescence (P) values at 42°C than at 25°C or 30°C (Figure 3a & b). In contrast, native species appeared showing similar patterns of Chl *a* transient curves at 25°C, 30°C, and 42°C (Figure 3c & d). At the same comparable temperature, the *Acacia* spp. seemed to show a higher P than the native species (Figure 3).

For each species investigated, there were no differences in φ_{PO} , φ_{EO} , φ_{DO} and Ψ_0 when they were subjected to 25°C and 30°C temperature treatments (data not shown). However, *Acacia*

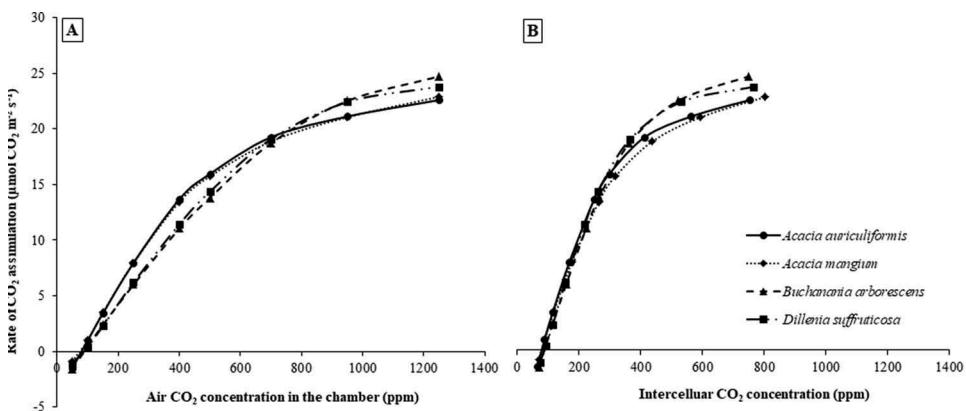


Figure 1. (A) CO₂ assimilation rates in response to air CO₂ concentration and (B) to intercellular CO₂ concentration of *Acacia* spp. and native species. $n = 6$, data are expressed as mean.

Table 1. Biochemical photosynthetic parameters at maximum (V_{cmax} and J_{max}) and at 400 ppm ambient CO_2 (A_c and A_j) of *Acacia* spp. and native species. Data are expressed as mean \pm standard deviation, $n = 6$; different letters indicate significantly different means among species at $P < 0.05$, V_{cmax} = maximum carboxylation rate of RuBisCO, J_{max} = potential electron transport rate for the regeneration of ribulose-1,5-bisphosphate, A_c = ribulose-1,5-bisphosphate-saturated CO_2 assimilation rate, A_j = ribulose-1,5-bisphosphate-limited CO_2 assimilation rate.

Species	V_{cmax} ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$)	J_{max} ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$)	A_c ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$)	A_j/A_c (arbitrary unit)
<i>Acacia auriculiformis</i>	112 \pm 6 ^{ab}	134 \pm 9 ^b	16.2 \pm 0.6 ^a	1.04 \pm 0.06 ^c
<i>Acacia mangium</i>	101 \pm 5 ^b	129 \pm 5 ^b	15.5 \pm 0.7 ^a	1.08 \pm 0.06 ^c
<i>Buchanania arborescens</i>	109 \pm 10 ^{ab}	151 \pm 8 ^a	13.9 \pm 0.9 ^b	1.25 \pm 0.06 ^a
<i>Dillenia suffruticosa</i>	120 \pm 10 ^a	149 \pm 9 ^a	15.0 \pm 0.8 ^{ab}	1.15 \pm 0.06 ^b
ANOVA				
F-value	5.5	11.4	9.1	15.1
P-value	<0.01	<0.001	<0.001	<0.001

Table 2. Observed and fitted (in parenthesis) instantaneous gas exchange parameters of *Acacia* spp. and native species measured at air CO_2 concentration of 400 ppm. Data are expressed as mean \pm standard deviation, $n = 6$; different letters indicate significantly different means among species at $P < 0.05$, A = CO_2 assimilation rate, g_s = stomatal conductance, E = transpiration rate, and WUE = water use efficiency.

Species	A ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$)	g_s ($\text{mol } H_2O \text{ m}^{-2} \text{ s}^{-1}$)	E ($\text{mmol } H_2O \text{ m}^{-2} \text{ s}^{-1}$)	WUE ($\mu\text{mol } CO_2 \text{ mmol}^{-1} H_2O$)
<i>Acacia auriculiformis</i>	(13.8 \pm 0.3)	(0.14 \pm 0.01)	(2.2 \pm 0.2)	(6.4 \pm 0.4)
<i>Acacia mangium</i>	(13.8 \pm 0.3)	(0.14 \pm 0.01)	(2.2 \pm 0.2)	(6.4 \pm 0.4)
<i>Buchanania arborescens</i>	13.4 \pm 0.5 ^a	0.23 \pm 0.01 ^a	3.3 \pm 0.2 ^a	4.0 \pm 0.2 ^b
<i>Dillenia suffruticosa</i>	(13.6 \pm 0.7)	(0.16 \pm 0.01)	(2.4 \pm 0.2)	(5.7 \pm 0.3)
ANOVA				
F-value	83.1	81.5	68.0	29.0
P-value	<0.001	<0.001	<0.001	<0.001
	(<0.001)	(<0.001)	(<0.001)	(<0.001)

spp. exhibited significant reductions of ϕ_{Po} , ϕ_{Eo} and Ψ_0 and a significant increase in ϕ_{Do} when they were under the treatment at 42°C compared at 30°C ($P < 0.001$, Figure 4). In contrast, both native species showed no difference in these parameters (ϕ_{Po} , ϕ_{Eo} , Ψ_0 , and ϕ_{Do}) when they were subjected to 42°C compared to 30°C ($P > 0.05$, Figure 4).

Under the same comparable temperature treatments, *Acacia* spp. had significantly higher ϕ_{Po} , ϕ_{Eo} , and Ψ_0 values, but a significantly lower ϕ_{Do} , than the native species ($P < 0.01$, Figure 4). There were no significant differences in the phyllode Chl *a* fluorescence parameters between *Acacia* spp. (i.e., *A. auriculiformis* vs. *A. mangium*) subjected to the same temperature treatments ($P > 0.05$). For the native species, *D. suffruticosa* had significantly higher ϕ_{Po} , ϕ_{Eo} , and Ψ_0 values, but a significantly lower ϕ_{Do} than *B. arborescens* when subjected to the same temperature treatments ($P < 0.05$).

Discussion

This study revealed that *Acacia* spp. exhibited higher rates of photosynthesis, which can be attributed to their greater g_s and ϕ_{Po} , and greater adjustment of photosynthetic apparatus to temperature changes compared to native species under the specific habitat conditions

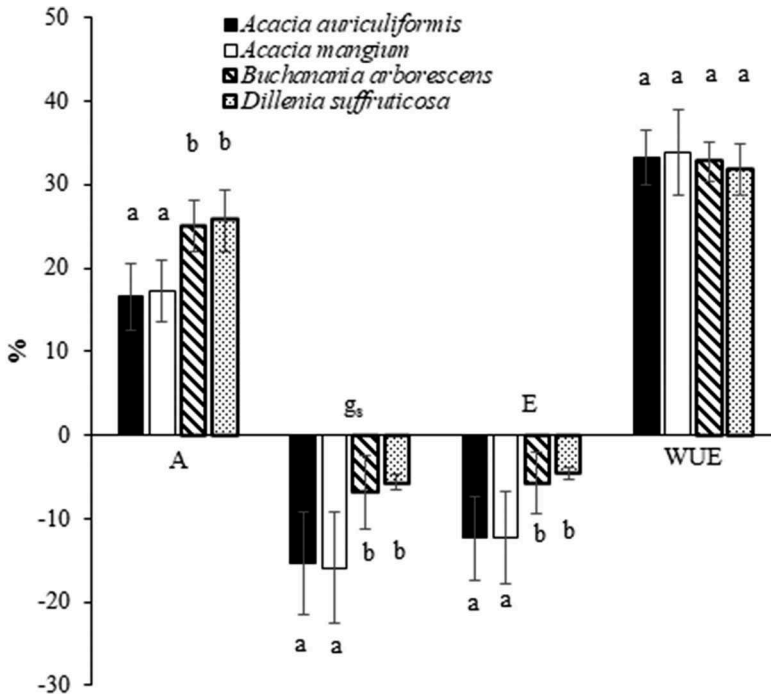


Figure 2. The variation in the instantaneous gas exchange parameters of *Acacia* spp. and native species induced by an increase in the air CO₂ concentration (from 400 to 500 ppm). n = 6, data are expressed as means ± standard deviations, different letters indicate significantly different means among species at P < 0.05, A = CO₂ assimilation rate, g_s = stomatal conductance, E = transpiration rate, and WUE = water use efficiency.

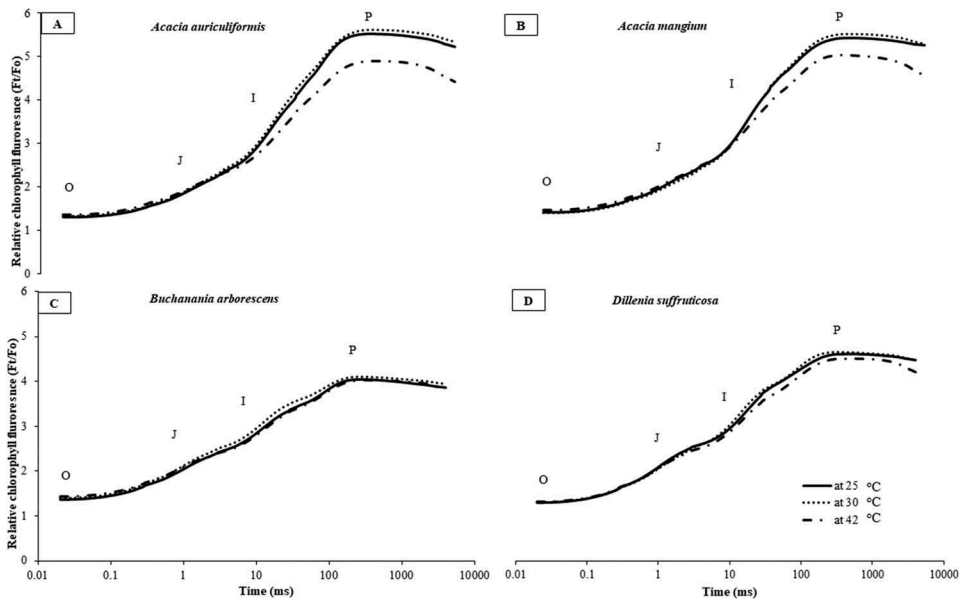


Figure 3. Chlorophyll *a* fluorescence transient curves of *Acacia* spp. and native species under different temperature treatments. n = 30, data are expressed as means; F₀ and F_t = fluorescence intensity at 0 s and time t, respectively; O, J and I = relative fluorescence intensities at 20 μs, 3 ms and 30 ms, respectively; P = relative maximal fluorescence.

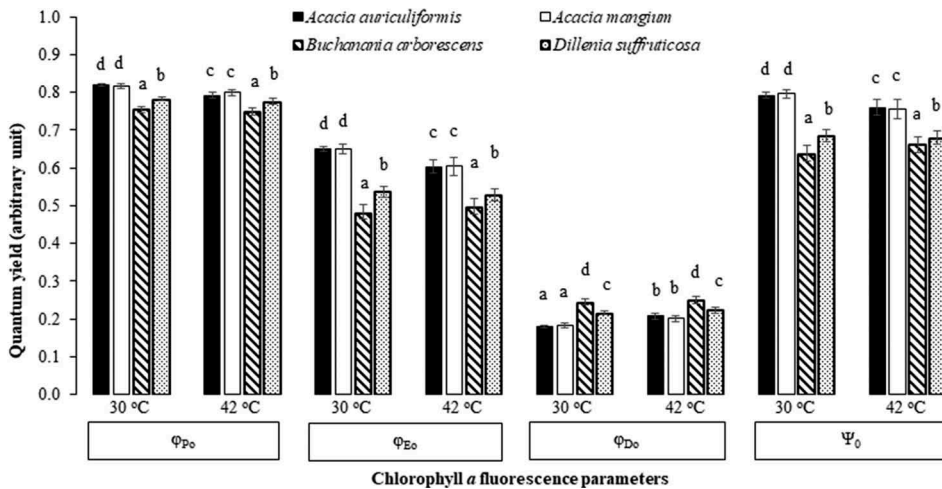


Figure 4. Chlorophyll *a* fluorescence quantum yields of *Acacia* spp. and native species under different temperature treatments. $n = 30$, data are expressed as means \pm standard deviations, different letters indicate significantly different means of the same parameters among species at $P < 0.05$, ϕ_{Po} = maximum quantum yield of primary photochemistry, ϕ_{Eo} = quantum yield of electron transport, ϕ_{Do} = quantum yield of energy dissipation, Ψ_o = probability that a trapped exciton moves an electron into the electron transport beyond the primary quinone acceptor of photosystem II.

investigated. The higher CO_2 assimilation rates, better light harvesting efficiency under comparable conditions and greater plasticity of PS II in response to temperature stress of *Acacia* spp. than native species may allow invasive species to maintain a competitive advantage over native vegetation at the post-establishment stage of invasion process and consequently establish monospecific stands at invaded ranges in the tropics.

A relatively large stomatal opening facilitates CO_2 diffusion from ambient air to sites of CO_2 assimilation in the chloroplast but also increases water loss (higher E) that may eventually lead to water deficiency in plants (Farquhar & Sharkey, 1982). Most plants under natural conditions respond to a lack of soil water by partly closing their stomata, with a trade-off of reduced A and E , but increased WUE (Escalona, Flexas, & Medrano, 2000; Farquhar & Sharkey, 1982; Gollan, Turner, & Schulze, 1985). Previous studies have reported no significant differences in the WUE between *Acacia* spp. (*A. longifolia* and *A. saligna*) and native vegetation, such as *Protea repens*, *Chrysanthemoides monilifera*, *Dodonaea viscosa* and *Leucadendron salignum* (Kraaij & Cramer, 1999; Peperkorn, Werner, & Beyschlag, 2005). In this study, we found that *Acacia* spp. follow a different strategy from native species in which invasive species maintain a higher stomatal opening level (denoted by higher g_s) to enable a higher A while retaining a higher E and lower WUE than the native species.

Transpiration rates of *Acacia* spp. are poorly documented (Morris et al., 2011). Here we found that *Acacia* spp. had higher E than native species, which is consistent with the patterns previously reported for *Acacia cyclops* in comparison with indigenous fynbos species in South Africa (Rutherford & Bösenberg, 1988). High transpiration rates facilitate nutrient acquisition, e.g., phosphorus (Pang et al., 2018), but also increase water loss. One possible mechanism that *Acacia* spp. may use to overcome the disadvantage of greater

water loss (denoted by the higher E compared with that of the native species) is to develop their greater root surface areas and longer root lengths than native plants (Lowe et al., 2000; Morris et al., 2011; Richardson & Rejmánek, 2011; Werner, Zumkier, Beyschlag, & Máguas, 2010).

Measurements of Chl *a* fluorescence and its multiphase transient (OJIP) are commonly used to probe photosynthetic performance (Murchie & Lawson, 2013; Papageorgiou & Govindjee, 2004). The typical range of ϕ_{Po} value is 0.75–0.85 in healthy, unstressed leaves (Björkman & Demmig, 1987; Bolhàr-Nordenkamp & Öquist, 1993; Méthy, Gillon, & Houssard, 1997) and under optimal conditions for most C_3 plants, the ϕ_{Po} value is typically 0.83 (Kalaji et al., 2014; Murchie & Lawson, 2013). Our data revealed that at both 25°C and 30°C, the ϕ_{Po} values of *Acacia* spp. (0.81–0.82) were closer to optimal ϕ_{Po} values of C_3 plants compared to the lower ϕ_{Po} values for native species (0.75–0.78). Further, we found no significant change in ϕ_{Po} values for the two native species when subjected to 25°C, 30°C and 42°C (0.75 for *B. arborescens* and 0.78 for *D. suffruticosa*). In contrast, the two *Acacia* spp. significantly decreased their ϕ_{Po} values (0.79 for *A. auriculiformis* and 0.80 for *A. mangium*) when they were subjected to 42°C compared to their ϕ_{Po} values at 25°C or 30°C (0.82 for *A. auriculiformis* at both temperatures; 0.81 and 0.82 for *A. mangium* at 25°C and 30°C, respectively). Yu and Ong (2002) also reported that the optimum temperature for photosynthetic CO_2 assimilation of *A. mangium* seedlings in Singapore was 30–32°C and no significant changes in their ϕ_{Po} values were recorded between the temperature range of 20–40°C.

Climate change induces physiological heat stress over short durations (hour to day scales) in plants and causes an imbalance between light-driven electron transport and carbon assimilation in most plants (Allen et al., 2010; Pachauri et al., 2014; Wujeska-Klaue, Bossinger, & Tausz, 2015). Notably in our study, at 25°C, 30°C, and 42°C, *Acacia* spp. consistently exhibited significantly higher ϕ_{Po} values than native species, suggesting that PSII systems of *Acacia* spp. harvest light better than the native species at temperatures investigated and thus, a greater plasticity of PSII in *Acacia* spp. We argue that the better adjustment in photosynthetic apparatus such as PSII in *Acacia* spp. to a broader temperature range (25–42°C) may allow *Acacia* spp. to maximize their photosynthetic capacity at more optimal temperatures (25–30°C) while also quickly protecting their photosynthetic apparatus from non-optimal temperatures (42°C) and heat stress. This plasticity would enable *Acacia* spp. to better perform at optimal temperatures and show higher survival under conditions of heat stress compared to native species, provided that leaf temperatures remain below the upper limit of acclimation for these species (Zhu et al., 2018). In contrast, the lack of plasticity of PSII for the native species would put them at a disadvantage over *Acacia* spp. particularly under elevated temperatures. It is likely that *Acacia* spp. will recover their maximum photosynthetic capacity faster than native species after removing heat stress conditions, however further studies are needed to support this.

A faster acquisition, or more efficient use, of resources facilitates the successful invasion of exotic plants (Cordell, Cabin, & Hadway, 2002; Durand & Goldstein, 2001; Funk & Vitousek, 2007). The key biological traits of *Acacia* spp. that indicate their ability to rapidly acquire resources are typically the substantial allocation to root mass, heteroblasty, and strong N_2 -fixation ability (Morris et al., 2011; Werner et al., 2010). Our study further demonstrated that a higher g_s along with the high light-harvesting efficiency and ability to better protect the photosynthetic apparatus against heat stress in *Acacia* spp. may also give them a competitive advantage over co-occurring native tree species at the post-establishment stage of *Acacia* spp.

invasion process in Bornean heath forests. Our study, using photosynthetic parameters, could also aid in projecting the future performance of invasive *Acacia* spp. in natural habitats in response to climate change associated with temperature fluctuations.

Our study may have some limitations since we only evaluated plant performance using instantaneous gas exchange parameters and *in situ* environmental leaf data, which may be different from whole plant response patterns. Thus, a concerted effort using an integrated approach to gather comparative ecophysiological information, such as water relations, mineral profiles, and growth data, over a few growing seasons is required to precisely determine whether these patterns are habitat-specific, and thus potentially influenced by the edaphic and habitat conditions in which these exotic *Acacia* spp. become established.

Our study was conducted at the post-establishment stage of *Acacia* spp. invasion in which invasive species have successfully established in invaded ranges. An exotic species can fail to become an invader if it cannot pass any one of the barriers at any stage of the invasion process, and invasion can fail even after the alien species has spread (Blackburn et al., 2011). Thus, our findings are crucial in that they provide some ecophysiological insights into understanding the mechanisms that may facilitate the further success of *Acacia* spp. invasion at the post-establishment stage. *Acacia* spp. are usually introduced into novel ranges for some initial ecological benefits such as land rehabilitation, and are typically neglected until they are naturalized, widely spread and cause negative impacts on invaded native ecosystems. An understanding of the competitive advantage of mature *Acacia* spp. over native tree species will aid in the selection of appropriate methods to mitigate the negative impacts of these invasive species, especially when other management methods such as prevention, eradication or containment do not appear to be effective (Pyšek & Richardson, 2010).

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