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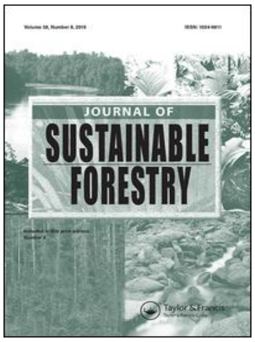

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Photosynthetic Responses of Invasive *Acacia Mangium* and Co-Existing NATIVE Heath Forest Species to Elevated Temperature and Co_2 Concentrations

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ABSTRACT

The impacts of climate change, in particular via elevated temperature and atmospheric CO_2 concentrations, cause differential photosynthetic responses between native and invasive alien plants, often resulting in varying magnitudes of plant growth and productivity. This study investigated variations in photosynthetic responses of an invasive alien *Acacia* species and two successional groups of tropical heath forest species: early secondary (*Buchanania arborescens* and *Dillenia suffruticosa*) and secondary (*Calophyllum inophyllum* and *Ploiarium alternifolium*) groups at elevated temperature (25to 30°C) and CO_2 levels (400 to 700 ppm). Invasive *A. mangium* appears better adapted to higher temperature and CO_2. High temperature improved CO_2 assimilation of *A. mangium* compared to heath species, which was attributed to increased transpiration rate and stomatal conductance but decreased water-use efficiency. Photosynthetic responses showed no differences in early secondary species at elevated temperature and CO_2 but invasive *A. mangium* and *P. alternifolium* were stimulated by elevated CO_2. The greater maximum net photosynthesis of *A. mangium* coincided with lower light compensation point and electron transport rate for RuBP regeneration, to a certain extent. Findings provide insights into possible underlying ecophysiological mechanisms contributing to the invasion success of Acacias in degraded tropical heath forests in response to future climate change.

KEYWORDS
Acacia; Borneo; climate change; CO_2 response curves; *Kerangas* forest; light response curves; photosynthesis

Introduction

Global climate change is a major concern to agriculture and forestry due to its impact on physiology and productivity of plants (Choi et al., 2017; Dusenge et al., 2019; Ehleringer et al., 1991; Eschenbach et al., 1998; Kallarackal & Roby, 2012; Lloyd & Farquhar, 2008; Peperkorn et al., 2005; Possell & Hewitt, 2009). In the context of plant invasions, elevated temperature and atmospheric CO_2 concentrations resulting from climate change have been shown to facilitate the spread of invasive plant species (Bradley et al., 2010; Hellmann et al., 2008). Many invasive plants benefit from elevated atmospheric CO_2

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concentrations (Liu et al., 2017), thus exacerbating the impacts of invasions on native ecosystems (Dukes & Mooney, 1999). Climate change can promote alien plant invasions either by accelerating growth and modifying ecophysiological responses of invasive species, or by increasing the competitive ability of invasive species over native species (Cai, 2011; Dukes, 2000; McDowell, 2002; Ruiz-Vera et al., 2013; Walther et al., 2009).

Leaf gas exchange measurements in response to variations in temperature and CO_2 concentration using a gas exchange system have provided insights into instantaneous photosynthetic parameters, such as net CO_2 assimilation rate (A), stomatal conductance (G_s), transpiration rate (E) and water-use efficiency (WUE), and biochemical parameters of leaf photosynthesis, such as Rubisco activity and electron transport capacity (Aleric & Kirkman, 2005; Farquhar & Sharkey, 1982, 1984; Golbeck & Est, 2014; Sharkey, 1985; Sharkey et al., 2007), and are widely used to determine underlying biochemical and physical limitations to photosynthesis (Long & Bernacchi, 2003; Sharkey, 2016). Both elevated atmospheric temperature and CO_2 levels generally affect plant photosynthetic performances (Eschenbach et al., 1998; Possell & Hewitt, 2009). In addition, the photosynthetic responses of invasive and noninvasive species to climate change vary (McDowell, 2002; Ruiz-Vera et al., 2013), with more problematic invasive species responding particularly strongly to elevated CO_2 levels (Dukes, 2000). Invasive species differ in key functional traits from co-existing native plants by having efficient dispersal mechanism, higher resource acquisition, superior colonization ability, rapid life cycle and reproduction, faster growth, broad eco-physiological niches, and extensive environmental tolerance and adaptability (Funk et al., 2016; Hellmann et al., 2008; Higgins & Richardson, 2014; Le Maitre et al., 2011; Mathakutha et al., 2019; Rejmánek & Richardson, 1996; Richardson & Rejmánek, 2011; Van Kleunen et al., 2010).

Among non-native plant species recorded in tropical east Asia, exotic *Acacia* species are increasingly becoming invasive (Corlett, 2010). Australian *Acacia* species were introduced to tropical Brunei Darussalam of Northwest Borneo in the 1990s for timber plantations and as roadside plantings (Osunkoya et al., 2005). Since their initial introduction, four *Acacia* species have been recorded (Sukri et al., 2018), with *Acacia mangium* documented as the most invasive *Acacia* species in Brunei Darussalam (Osunkoya & Damit, 2005). Degraded tropical and coastal heath forest communities in Brunei Darussalam have been most heavily affected by *Acacia* invasion (Din et al., 2015; Tuah, 2014) as the nitrogen (N_2)-fixing *Acacia* species are able to establish themselves in forests with nutrient-poor sandy soils (Brunig, 1974; Ghazoul & Sheil, 2010), outcompeting and displacing native plant species (Osunkoya et al., 2005). These invaded coastal heath forests become heavily dominated by *Acacia*, with co-occurring remnant native heath forest species and native secondary species (Osunkoya & Damit, 2005; Tuah, 2014).

Acacia species are typically associated with traits that are fundamental at early stages of succession (Aguilera et al., 2015; Koutika & Richardson, 2019), and thus can tolerate and adapt to a wide gradient of low to high light intensities, showing greater relative growth rates and more efficient net photosynthetic rates (Peperkorn et al., 2005). For example, both *Acacia auriculiformis* and *Acacia mangium* recorded increased photosynthetic responses in the form of stomatal conductance (G_s), transpiration rate (E) and saturated net photosynthesis (A_{max}) when grown under high irradiances (1500 μmol (photon) m^{-2} s^{-1}) and temperature of 30–32°C (Le et al., 2016a, 2016b, 2019; Yu & Ong, 2002). The N_2-fixing capacity of *Acacia* species results in greater leaf N per unit area or unit mass and leaf mass area (LMA) but they may experience lower photosynthetic N-use efficiency (PNUE) due to their inability in allocating N to photosynthetic mechanism, particularly during unlimited supplies of water and N resources (Novriyanti et al., 2012). In contrast, the responses of native tropical plants to variation of temperature and light are species-specific (Bazzaz & Pickett, 1980; Davies & Semui, 2006), and may depend on their successional groups (Khurana & Singh, 2001; Ribeiro et al., 2005), such as early successional group and late successional group (Swaine & Whitmore, 1988). For example, enhanced photosynthetic traits, such as A_{max}, G_s and dark respiration (R_d) were reported for nine sympatric pioneer tree species of Bornean *Macaranga* under high light irradiances (Davies, 1998). In a pot experiment, the early secondary tropical tree, *Astronium graveolens*, showed higher values of CO_2 assimilation (A) and E rates compared to the secondary and shade-tolerant species, *Cariniana legalis* (Ribeiro et al., 2005).

Understanding variations in photosynthetic responses of invasive plants and native plants from different successional groups to elevated temperature and atmospheric CO_2 concentration can assist policymakers in predicting risks from plant invaders and developing effective forest management strategies. Here, we examined the photosynthetic responses of invasive *Acacia mangium* Willd. and native heath forest plants from different successional groups (*i.e.* early secondary and secondary species). Specifically, we investigated the effects of elevated temperature (25°C and 30°C) or CO_2 concentrations (400 and 700 ppm) separately on various instantaneous leaf gas exchange and biochemical parameters of photosynthesis between *A. mangium* and, native early secondary and secondary heath forest species. We formulated two hypotheses on differential photosynthetic responses:

(1) Invasive *A. mangium* will exhibit increased photosynthetic capacity with elevated temperature and CO_2 compared to native heath species because invasive plants have broader range of environmental adaptability and tolerance.
(2) Photosynthetic responses of early secondary plant species, but not secondary species, will be positively affected by elevated temperature and CO_2 because early secondary species have traits associated with early stages of succession, similar to invasive species.

Materials and methods

Study site and species

This study was conducted within secondary coastal heath (*Kerangas*) forests (N 04°57.388, E 114°52.194; elevation 60 m *a.s.l*) near Universiti Brunei Darussalam in Brunei Darussalam, Northwest Borneo from June to August 2015. Brunei Darussalam recorded a mean annual temperature of 28.8°C and a total annual rainfall of 3714 mm in 2015, which were recorded at the Brunei International Airport, located *c.a.* 14 km away from the study site (Brunei Darussalam Meteorological Department, *unpublished data*). The Bornean heath forest is a unique type of aseasonal lowland rainforest that develop primarily on podzolized, highly acidic, sandy soils with low macronutrient contents (Ghazoul & Sheil, 2010; Ibrahim, 2020; Jaafar et al., 2016; N. N Rosli, 2016). The main soil properties of Bornean heath forests, particularly at the study sites are presented in Table 1.

Table 1. Differences in soil properties at depths (0–20 cm) of *Acacia*-invaded (disturbed) and non-invaded sites (undisturbed) in coastal heath forests of Brunei Darussalam. Data are expressed as mean ± standard error, SE (n = 6 plots per habitat). All values were reported in Ibrahim (2020) and N. N Rosli (2016).

Soil Variables	*Acacia*-invaded heath forest	Non-invaded heath forest
pH	4.93 ± 0.06	4.65 ± 0.09
Exchangeable K (mg kg^{-1})	0.03 ± 0.004	0.057 ± 0.01
Exchangeable Ca (mg kg^{-1})	0.01 ± 0.002	0.021 ± 0.004
Exchangeable Mg (mg kg^{-1})	0.033 ± 0.007	0.041 ± 0.011
Total N (g kg^{-1})	0.860 ± 0.030	0.670 ± 0.020
Total P (g kg^{-1})	0.26 ± 0.03	0.21 ± 0.05
Gravimetric water content (%)	8.20 ± 0.60	11.33 ± 0.59
Temperature (°C)	28.40 ± 0.19	27.22 ± 0.03

At the study site, secondary heath forests co-occur with *Acacia*-invaded habitats in patches within a background of urban and settlement areas (Figure 1; see also Yusoff et al., 2019). Invasive *Acacia mangium, A. auriculiformis* and *A. holosericea* in the study sites were found to co-exist with secondary heath forest species, such as *Dillenia suffruticosa, Ploiarium alternifolium, Melastoma malabathricum, Symplocos polyandra, Buchanania arborescens, Calophyllum inophyllum* and *Calophyllum soulatrri* (Tuah, 2014). A 100 m line transect radiating at 280° from North in the *Acacia*-invaded sites was established within the heath forest, following methods by Buckland et al. (2007). Along the line transect, three trees (6–8 m in height) for each plant species were randomly chosen, with selected trees *c.a.* 10 m apart from each other.

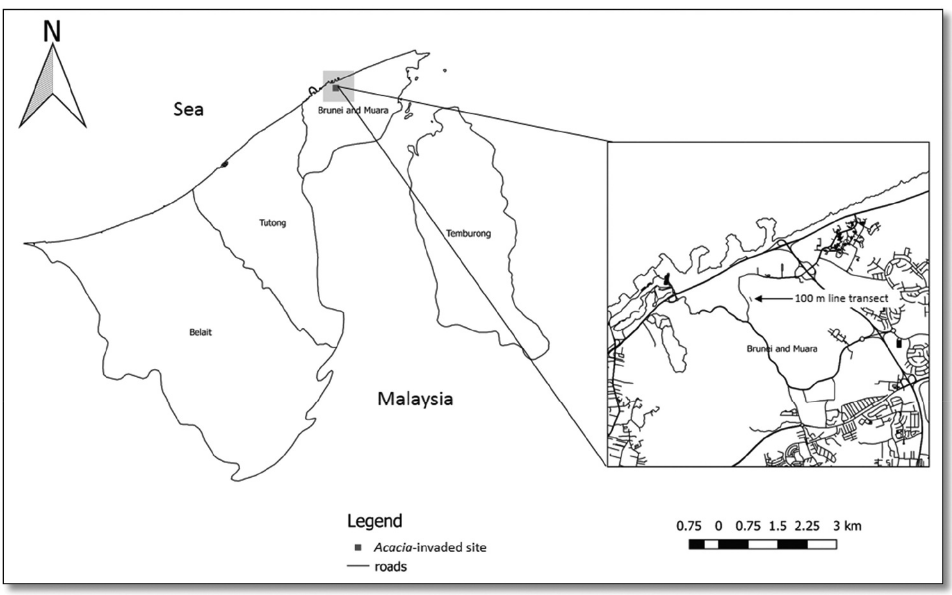

Figure 1. Location of the study site. A 100 m line transect in *Acacia*-invaded sites within coastal heath forest in the Brunei-Muara district of Brunei Darussalam was set up.

A total of five plant species were selected and investigated for this study: *Acacia mangium* Willd. (the invasive species) and *Buchanania arborescens* (Blume) Blume, *Dillenia suffruticosa* (Griff.) Martelli, *Calophyllum inophyllum* L. and *Ploiarium alternifolium* (Vahl) Melch (the native heath forest species). *Acacia mangium* was the most dominant invasive *Acacia* species at the study site, while the four selected native species were commonly found co-occurring with *Acacia* species at these study sites and in other disturbed coastal heath forests in Brunei Darussalam (Tuah, 2014). We classified the four selected native species into two successional groups based on their growth performances and shade adaptation (Bazzaz & Pickett, 1980; Davies & Semui, 2006; Raaimakers et al., 1995; Ribeiro et al., 2005). Similar to *A. mangium*, early secondary plant species (*B. arborescens* and *D. suffruticosa*) are generally light-demanding and exhibit faster growth than secondary plant species (*C. inophyllum* and *P. alternifolium*), which are more shade-tolerant (Kartawinata et al., 2008; Ribeiro et al., 2005; Tuah, 2014; Le et al., 2019). *Acacia mangium* (Fabaceae) is an evergreen fast-growing tree native to parts of Indonesia, Papua New Guinea and Australia (Koutika & Richardson, 2019), which can grow up to 30 m tall (Hedge et al., 2013; Slik, 2009; Yu & Ong, 2002). *Buchanania arborescens* (Anacardiaceae) is an evergreen, drought-tolerant tree (*c.a.* 35–40 m) typical of heath forest and open grasslands, belonging to early secondary successional group (Koh et al., 2009; Nelson et al., 2007; Slik, 2009). *Dillenia suffruticosa* (Dilleniaceae) is a large, hardy, and extremely high light-demanding pioneer shrub (*c.a.* 10 m tall), growing mainly in secondary forests and open areas (Davies & Semui, 2006; H. R. Rosli, 2014; Slik, 2009). The two secondary species are slow-growing species typical of coastal heath and secondary forests with sandy soils but *C. inophyllum* (Calophyllaceae) is a medium-sized to a large evergreen tree (*c.a.* 8–30 m) (Lim, 2012; Slik, 2009), while *P. alternifolium* (Bonnetiaceae) is an understory tree species between 4 and 13 m tall (Hashim et al., 2016; Osunkoya et al., 2005). Based on their growth environment and life form type, all study species here, including *Acacia mangium* have heterobaric leaves that typically display a degree of stomatal patchiness and non-uniform leaf photosynthesis specifically during dry conditions (Kenzo et al., 2007; Sommerville et al., 2012; Terashima, 1992). However, during the study period (June–August 2015), there were moderate to high monthly rainfall levels (ranging from 226.9 mm in June to 308.6 mm in August) and target trees did not show any obvious signs of wilting or drought-stress.

Ex-situ leaf gas exchange measurements

Two twigs from each of three mature and healthy individuals (n = 3) of *A. mangium, B. arborescens, C. inophyllum, D. suffruticosa* and *P. alternifolium* were collected for ex-situ leaf gas exchange measurements. Only twigs with fully expanded leaves, consistently exposed to sunlight during sunny days were collected from the tree top (at *c. a.* 5 m height) in the morning (between 9:30 am until 12 noon) as described in Le et al. (2016a, 2016b, 2019) and Weerasinghe et al. (2014). Leaf gas exchange measurements were immediately conducted on leaves using a portable, open-flow gas exchange system fitted with a 2 × 3 cm chamber and an LED lamp as the light source (LI-6400XT, LI-COR Inc., USA). The leaves were clamped into the chamber and left to stabilize to the measuring conditions for 15 to 30 minutes or until CO_2 assimilation rate and stomatal conductance values were steady.

Photosynthetic light response (A-L_i) curves of the leaves were developed under a set of photosynthetic photon flux density (PPFD) values of 10, 40, 60, 120, 250, 500, 1000, 1500, and 1800 μmol (photon) m^{-2} s^{-1} at a relative humidity of 50–60% and CO_2 concentration of 400 ppm inside the chamber. The leaf temperature in the chamber was maintained at either 25°C or 30°C as the mean leaf temperature in the study sites ranges from 26.5°C to 29.0°C. Photosynthetic CO_2 response (A-C_i) curves were also developed under varying CO_2 concentration values of 50, 100, 150, 250, 380, 500, 700, 950, and 1250 ppm at a relative humidity of 50–60%, PPFD of 1500 μmol (photon) m^{-2} s^{-1} and 25°C inside the chamber.

The instantaneous leaf gas exchange parameters were measured at a PPFD of 1500 μmol m^{-2} s^{-1}, CO_2 concentration of 400 ppm and leaf temperature of 25°C and 30°C as well as at a PPFD of 1500 μmol m^{-2} s^{-1}, leaf temperature of 25°C and CO_2 concentration of 400 and 700 ppm. Net CO_2 assimilation rates (A, μmol CO_2 m^{-2} s^{-1}), transpiration rates (E, mmol H_2O m^{-2} s^{-1}) and stomatal conductance (G_s, mol H_2O m^{-2} s^{-1}) were directly obtained from the portable gas exchange system, while the water-use efficiency (WUE, μmol CO_2 $mmol^{-1}$ H_2O) was calculated from the A/E ratio following Farquhar and Richards (1984).

Maximum net photosynthesis or light-saturated photosynthesis (A_{max}, μmol CO_2 m^{-2} s^{-1}), apparent quantum yield (A_{qe}, $μmol^{-1}$ quantum), light compensation point (LCP, $μmol^{-1}$ quantum m^{-2} s^{-1}), maximum carboxylation rate of Rubisco (V_{cmax}, μmol CO_2 m^{-2} s^{-1}) and potential electron transport rate for Ribulose-1,5-bisphosphate (RuBP) regeneration (J; μmol CO_2 m^{-2} s^{-1}) based on CO_2 response curves at 25°C and PPFD of 1500 μmol (photon) m^{-2} s^{-1} were calculated using the formulae by Aleric and Kirkman (2005), and Sharkey et al. (2007). We used a nonlinear mixed models procedure in Statistical Analysis System (SAS) Version 9.2 (Statistical Analysis System [SAS], 2009) to fit curves of photosynthetic data for each plant species. We then estimated A_{max}, V_{cmax} and J using analysis of parameter estimation PROC NONLIN in SAS (Peek et al., 2002).

Statistical analysis

A two-way Analysis of Variance (ANOVA) was used to evaluate the effect of species, temperature or CO_2 concentrations, and their interactions on variables of instantaneous gas exchange performances (A, E, G_s and WUE). Significant pairwise differences were then further analyzed by using Tukey's tests. One-way ANOVA was used to evaluate between-species differences in biochemical photosynthetic parameters (A_{max}, A_{qe}, LCP, V_{cmax} and J). All tests utilized sample size of $n = 3$ trees per species. Assumptions of normality and heterogeneity of variances were tested, and were not violated. All statistical analysis was conducted using SAS Version 9.2 (Statistical Analysis System [SAS], 2009).

Results

Variation in photosynthetic light response curves and photosynthetic performances at leaf temperatures of 25 and 30ºC

Photosynthetic light response curves at 25°C and CO_2 concentration of 400 ppm showed *C. inophyllum* apparently recorded the highest photosynthetic capacities, followed by *P. alternifolium, D. suffruticosa* and *A. mangium*, while *B. arborescens* had the lowest photosynthetic capacities (Figure 2). Contrastingly, at 30°C, the invasive *A. mangium* seemingly showed the highest photosynthetic capacities, followed by early secondary species (*B. arborescens* and *D. suffruticosa*), and secondary species, with *P. alternifolium* had the lowest photosynthetic capacities (Figure 2).

To evaluate variations in the instantaneous gas exchange performance parameters (A, E, G_s and WUE) of invasive *A. mangium* and native heath species, data obtained at PPFD of 1500 μmol (photon) m^{-2} s^{-1} and CO_2 concentration of 400 ppm at 25°C and 30°C were used (Table 2). The effects of species, temperature, and their interactions were significant on all parameters except G_s (Table 2). The results showed that at 25°C, invasive *A. mangium* showed significantly lower A and E compared to the native species, particularly the secondary species. In contrast, at 30°C, *A. mangium* recorded significantly greater A and E than the native heath species and *A. mangium* at 25°C. The A between early secondary species demonstrated no significant differences at both temperatures. Both A and E of secondary species, and E of early secondary species (*B. arborescens* only) were reduced at elevated temperature (30°C).

Stomatal conductance (G_s) of *A. mangium* was significantly lower than G_s of the early secondary species, *D. suffruticosa* but not significantly different from other species at 25°C (Table 2). However, at 30°C, *A. mangium* showed significantly higher G_s than all four native species and that of *A. mangium* itself at 25°C. Both *D. suffruticosa* and *P. alternifolium* recorded significant lower G_s at increased temperature, while G_s for *B. arborescens* and *C. inophyllum* did not differ significantly at both temperatures. *Acacia mangium* was reported to have higher WUE than *P. alternifolium* (secondary species) at 25°C but was similar to other species. However, at 30°C, the invasive *A. mangium* recorded significantly lower WUE than *B. arborescens* and *P. alternifolium* but did not differ significantly with the others. The WUE values were significantly lower at 30°C than at 25°C for *A. mangium* and *D. suffruticosa* only but vice versa for *P. alternifolium*.

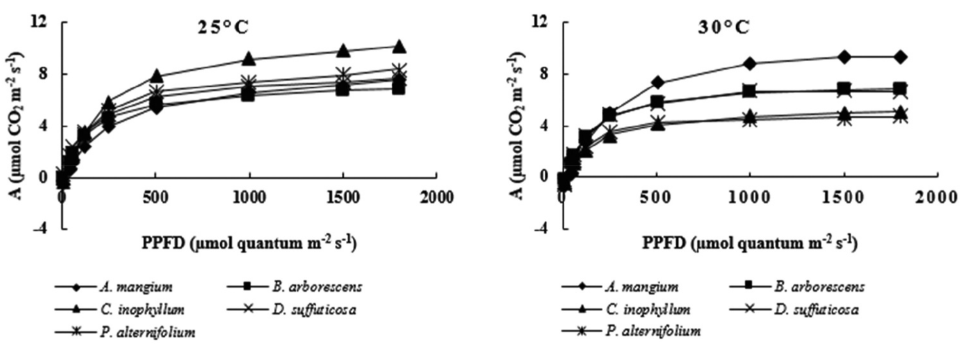

Figure 2. Photosynthetic light response (A-L_i) curves of invasive *Acacia mangium* and four co-occurring tropical species (*Buchanania arborescens* and *Dillenia suffruticosa* of early secondary species and, *Calophyllum inophyllum* and *Ploiarium alternifolium* of secondary species) in Brunei's coastal heath forest, measured at a constant CO_2 concentration of 400 ppm and leaf temperature of either 25 or 30°C. The data are expressed as mean values (*n* = 3 trees per species) but standard error values are excluded for ease of data interpretation.

Table 2. Variation in instantaneous gas exchange performances (net CO_2 assimilation rate or A, µmol CO_2 m^{-2} s^{-1}; transpiration rate or E, mol H_2O m^{-2} s^{-1}; stomatal conductance or G_s, mmol H_2O m^{-2} s^{-1} and water-use efficiency or WUE, µmol CO_2 $mmol^{-1}$ H_2O) of invasive *Acacia mangium* and four tropical species (*Buchanania arborescens* and *Dillenia suffruticosa* of early secondary species and, *Calophyllum inophyllum* and *Ploiarium alternifolium* of secondary species) in Brunei's coastal heath forest. Measurements were made at a photosynthetic photon flux density (PPFD) of 1500 µmol (photon) m^{-2} s^{-1}, CO_2 concentration of 400 ppm and leaf temperature of either 25°C or 30°C. The data were expressed as means ± standard error, SE (*n* = 3 trees per species). A two-way ANOVA on the effects of study species (*A. mangium, B. arborescens, C. inophyllum, D. suffruticosa*, and *P. alternifolium*) and leaf temperature regimes (25°C and 30°C) on A, E, G_s, and WUE were conducted at 5% significance level, which was indicated by *: $p < .05$; **: $p < .01$; ***: $p < .001$, ns: no significant. Note: Means with different lowercase letters within the same row showed significant differences between temperatures within a species, while means with different uppercase letters within the same column showed significant differences between species.

		Net CO_2 assimilation rate (A) (µmol CO_2 m^{-2} s^{-1})				
Type	Species	Temperature		F-value		
		25°C	30°C	Species	Temperature	Species x temperature
a) Invasive	*A. mangium*	6.78 ± 0.04$^{b, C}$	9.04 ± 0.47$^{a, A}$	5.83**	53.39***	38.38***
b) Early secondary	*B. arborescens*	6.99 ± 0.21$^{a, BC}$	6.70 ± 0.41$^{a, B}$			
	D. suffruticosa	7.77 ± 0.07$^{a, B}$	6.62 ± 0.37$^{a, B}$			
c) Secondary	*C. inophyllum*	8.77 ± 0.20$^{a, A}$	5.08 ± 0.50$^{b, B}$			
	P. alternifolium	9.01 ± 0.07$^{a, A}$	4.59 ± 0.35$^{b, B}$			
		Transpiration rate (E) (mol H_2O m^{-2} s^{-1})				
a) Invasive	*A. mangium*	0.99 ± 0.10$^{b, C}$	2.02 ± 0.03$^{a, A}$	7.09**	7.11*	22.53***
b) Early secondary	*B. arborescens*	1.10 ± 0.03$^{a, BC}$	0.96 ± 0.02$^{b, BC}$			
	D. suffruticosa	1.56 ± 0.19$^{a, AB}$	1.39 ± 0.18$^{a, B}$			
c) Secondary	*C. inophyllum*	1.74 ± 0.07$^{a, A}$	0.97 ± 0.08$^{b, BC}$			
	P. alternifolium	1.50 ± 0.14$^{a, ABC}$	0.66 ± 0.09$^{b, C}$			
		Stomatal conductance (G_s) (mmol H_2O m^{-2} s^{-1})				
a) Invasive	*A. mangium*	0.07 ± 0.008$^{b, BC}$	0.15 ± 0.012$^{a, A}$	17.88***	3.47ns	15.63***
b) Early secondary	*B. arborescens*	0.05 ± 0.010$^{a, C}$	0.04 ± 0.003$^{a, B}$			
	D. suffruticosa	0.14 ± 0.017$^{a, A}$	0.07 ± 0.012$^{b, B}$			
c) Secondary	*C. inophyllum*	0.04 ± 0.005$^{a, C}$	0.05 ± 0.007$^{a, B}$			
	P. alternifolium	0.11 ± 0.008$^{a, AB}$	0.04 ± 0.003$^{b, B}$			
		Water-use efficiency (WUE) (µmol CO_2 $mmol^{-1}$ H_2O)				
a) Invasive	*A. mangium*	6.82 ± 0.28$^{a, AB}$	4.80 ± 0.03$^{b, B}$	7.01**	8.58**	10.02***
b) Early secondary	*B. arborescens*	7.20 ± 0.73$^{a, A}$	6.04 ± 0.34$^{a, A}$			
	D. suffruticosa	6.15 ± 0.26$^{a, ABC}$	4.79 ± 0.44$^{b, B}$			
c) Secondary	*C. inophyllum*	4.99 ± 0.06$^{a, BC}$	5.44 ± 0.20$^{a, AB}$			
	P. alternifolium	4.86 ± 0.02$^{b, C}$	6.46 ± 0.30$^{a, A}$			

Variation in photosynthetic CO_2 response curve and photosynthetic performances at CO_2 concentrations of 400 and 700 ppm

Photosynthetic CO_2 response curves at 25°C and constant photosynthetic photon flux density (PPFD) of 1500 µmol (photon) m^{-2} s^{-1} apparently showed *P. alternifolium* (early secondary species) recorded the highest photosynthetic capacities, followed by *A. mangium, B. arborescens, C. inophyllum*, while *D. suffruticosa* seemingly showed the lowest photosynthetic capacities (Figure 3).

Variations of the instantaneous gas exchange performance parameters (A, E, G_s and WUE) of invasive *A. mangium* and native heath species at CO_2 concentrations of 400 and 700 ppm were evaluated using data obtained at 1500 µmol (photon) m^{-2} s^{-1} PPFD and 25°C (Table 3). Similar to the effects of temperature, the effects of species, CO_2 concentration, and their interactions were significant on all parameters except G_s (Table 3). At ambient CO_2 concentration (400 ppm), invasive *A. mangium* recorded significantly lower A than

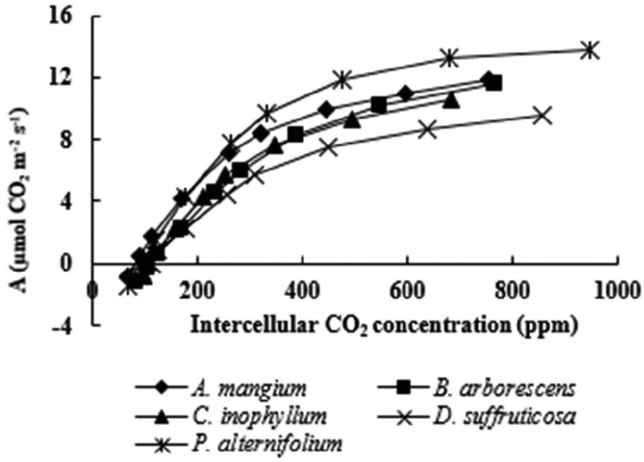

Figure 3. Photosynthetic CO_2 response (A-C_i) curves of invasive *Acacia mangium* and four co-occurring tropical species (*Buchanania arborescens* and *Dillenia suffruticosa* of early secondary species and, *Calophyllum inophyllum* and *Ploiarium alternifolium* of secondary species) in Brunei's coastal heath forest, measured at constant photosynthetic photon flux density of 1500 μmol (photon) m^{-2} s^{-1} and leaf temperature of 25°C. The data are expressed as mean values (n = 3 trees per species) but standard error values are excluded for ease of data interpretation.

D. suffruticosa and secondary species but was similar to *B. arborescens*. In contrast, at elevated CO_2 concentration (700 ppm), the A of *A. mangium* and *P. alternifolium* increased relative to the other species, and the values were significantly higher at 700 ppm than at 400 ppm. The A values of early secondary species and *C. inophyllum* were not significantly different between 400 and 700 ppm.

At 400 ppm, *A. mangium* showed significantly lower E than *D. suffruticosa* and secondary species but was similar to *B. arborescens* (Table 3). *Acacia mangium* also recorded significantly lower G_s than *D. suffruticosa* but did not differ with the others at 400 ppm. However, at elevated CO_2 concentration, both E and G_s of all species, including *A. mangium*, were significantly lower than *P. alternifolium*. Invasive *A. mangium* and *P. alternifolium* were not significantly different in E between CO_2 concentrations but early secondary species and *C. inophyllum* significantly decreased E at elevated CO_2. However, for G_s, only *D. suffruticosa* had lower values at increased CO_2 but vice versa for *P. alternifolium*. All study species recorded significantly increased WUE values at elevated CO_2. At 400 ppm, the invasive *A. mangium* recorded significantly greater WUE than *P. alternifolium* but significantly similar WUE with the other species at 700 ppm.

Comparison of photosynthetic capacities and related parameters of response curve between invasive Acacia mangium and tropical heath species

All the biochemical photosynthetic response curve parameters significantly differed between invasive and native heath species, except A_{qe} and V_{cmax} at 25°C and PPFD of 1500 μmol (photon) m^{-2} s^{-1} (Table 4). *Ploiarium alternifolium* (secondary species) recorded significantly greater A_{max} than early secondary species but similar to invasive *A. mangium* and its counterpart, *C. inophyllum*. Meanwhile, LCP values of *A. mangium* and

Table 3. Variation in instantaneous gas exchange performances (net CO_2 assimilation rate or A, μmol CO_2 m^{-2} s^{-1}; transpiration rate or E, mol H_2O m^{-2} s^{-1}; stomatal conductance or G_s, mmol H_2O m^{-2} s^{-1} and water-use efficiency or WUE, μmol CO_2 $mmol^{-1}$ H_2O) of invasive *Acacia mangium* and four tropical species (*Buchanania arborescens* and *Dillenia suffruticosa* of early secondary species and, *Calophyllum inophyllum* and *Ploiarium alternifolium* of secondary species) in Brunei's coastal heath forest. Measurements were made at a photosynthetic photon flux density (PPFD) of 1500 μmol (photon) m^{-2} s^{-1}, leaf temperature of 25°C and CO_2 concentration (CO_2 conc.) of either 400 or 700 ppm. The data were expressed as means ± standard error, SE (n = 3 trees per species). A two-way ANOVA on the effects of study species (*A. mangium, B. arborescens, C. inophyllum, D. suffruticosa*, and *P. alternifolium*) and CO_2 concentration (400 and 700 ppm) on A, E, G_s and WUE were conducted at 5% significance level, which was indicated by *: $p < .05$; **: $p < .01$; ***: $p < .001$, ns: no significant. Note: Means with different lowercase letters within the same row showed significant differences between CO_2 concentrations within a species, while means with different uppercase letters within the same column showed significant differences between species.

Type	Species	CO_2 concentration		F-value		
		400 ppm	700 ppm	Species	CO_2 conc.	Species x CO_2 conc.
		Net CO_2 assimilation rate (A) (μmol CO_2 m^{-2} s^{-1})				
a) Invasive	*A. mangium*	$6.78 \pm 0.05^{b, C}$	$11.15 \pm 0.21^{a, A}$	35.76***	29.40***	25.07***
b) Early secondary	*B. arborescens*	$6.99 \pm 0.21^{a, BC}$	$6.11 \pm 0.37^{a, C}$			
	D. suffruticosa	$7.77 \pm 0.07^{a, B}$	$7.75 \pm 0.50^{a, BC}$			
c) Secondary	*C. inophyllum*	$8.77 \pm 0.19^{a, A}$	$9.18 \pm 0.54^{a, B}$			
	P. alternifolium	$9.01 \pm 0.07^{b, A}$	$11.02 \pm 0.35^{a, A}$			
		Transpiration rate (E) (mol H_2O m^{-2} s^{-1})				
a) Invasive	*A. mangium*	$0.99 \pm 0.10^{a, C}$	$1.05 \pm 0.01^{a, B}$	9.08***	10.76**	6.82**
b) Early secondary	*B. arborescens*	$1.10 \pm 0.02^{a, BC}$	$0.58 \pm 0.14^{b, B}$			
	D. suffruticosa	$1.56 \pm 0.19^{a, A}$	$0.87 \pm 0.19^{b, B}$			
c) Secondary	*C. inophyllum*	$1.17 \pm 0.18^{a, AB}$	$0.69 \pm 0.06^{b, B}$			
	P. alternifolium	$1.50 \pm 0.13^{a, AB}$	$2.05 \pm 0.38^{a, A}$			
		Stomatal conductance (G_s) (mmol H_2O m^{-2} s^{-1})				
a) Invasive	*A. mangium*	$0.07 \pm 0.008^{a, BC}$	$0.08 \pm 0.002^{a, B}$	23.72***	0.13ns	10.73***
b) Early secondary	*B. arborescens*	$0.05 \pm 0.011^{a, C}$	$0.04 \pm 0.010^{a, B}$			
	D. suffruticosa	$0.14 \pm 0.01^{a, A}$	$0.06 \pm 0.010^{b, B}$			
c) Secondary	*C. inophyllum*	$0.04 \pm 0.005^{a, C}$	$0.05 \pm 0.004^{a, B}$			
	P. alternifolium	$0.11 \pm 0.010^{b, AB}$	$0.18 \pm 0.030^{a, A}$			
		Water-use efficiency (WUE) (μmol CO_2 $mmol^{-1}$ H_2O)				
a) Invasive	*A. mangium*	$6.82 \pm 0.28^{b, AB}$	$10.68 \pm 0.11^{a, AB}$	5.63**	52.22***	2.72*
b) Early secondary	*B. arborescens*	$7.20 \pm 0.73^{b, A}$	$13.02 \pm 2.25^{a, A}$			
	D. suffruticosa	$6.15 \pm 0.26^{b, ABC}$	$9.60 \pm 1.02^{a, AB}$			
c) Secondary	*C. inophyllum*	$4.99 \pm 0.02^{b, BC}$	$12.89 \pm 0.32^{a, A}$			
	P. alternifolium	$4.86 \pm 0.06^{b, C}$	$6.80 \pm 0.61^{a, B}$			

P. alternifolium were significantly lower than early secondary species and *C. inophyllum*. However, *D. suffruticosa* showed significantly lower J values than other species, including secondary species but similar J to *A. mangium*.

Discussion

Our findings on photosynthetic light response curves clearly revealed differential patterns of photosynthetic performances at contrasting leaf temperatures (25 and 30°C) among the three different plant groups (*i.e.* invasive species, and successional groups of early secondary and secondary species). At 25°C, the secondary species' response curves dominated higher photosynthetic capacities, followed by invasive *A. mangium* and early secondary species. However, when the leaf temperature was increased (30°C), the invasive *A. mangium* showed higher photosynthetic capacities compared to heath species. Enhanced photosynthetic

Table 4. Biochemical photosynthetic parameters (maximum net photosynthesis or light-saturated photosynthesis or A_{max}, mmol CO_2 m^{-2} s^{-1}; apparent quantum yield or A_{qe}, μmol CO_2 $μmol^{-1}$ quantum; light compensation point or LCP, $μmol^{-1}$ quantum m^{-2} s^{-1}; maximum carboxylation rate of Rubisco or V_{cmax}, μmol CO_2 m^{-2} s^{-1} and potential electron transport rate for Ribulose-1, 5-bisphosphate (RuBP) regeneration or J, μmol CO_2 m^{-2} s^{-1}) of the invasive *Acacia mangium* and four tropical species (*Buchanania arborescens* and *Dillenia suffruticosa* of early secondary species and, *Calophyllum inophyllum* and *Ploiarium alternifolium* of secondary species) in Brunei's coastal heath forests at 25°C and PPFD of 1500 μmol (photon) m^{-2} s^{-1}. Values were expressed as means ± standard error, SE (n = 3 trees per species). Different letters within the same column indicated significantly different means at $p < .05$ using a Tukey's test.

Group	Species	A_{max}	A_{qe}	LCP	V_{cmax}	J
Invasive	*A. mangium*	12.00 ± 0.34[ab]	0.0043 ± 0.0003[a]	75.23 ± 0.53[b]	28.86 ± 0.95[a]	94.43 ± 2.23[ab]
Early secondary	*B. arborescens*	10.43 ± 0.45[b]	0.0051 ± 0.0001[a]	107.45 ± 3.52[a]	30.52 ± 2.16[a]	108.16 ± 4.57[a]
	D. suffruticosa	11.36 ± 0.16[b]	0.0042 ± 0.0001[a]	102.57 ± 2.27[a]	25.22 ± 0.37[a]	92.54 ± 1.29[b]
Secondary	*C. inophyllum*	11.81 ± 0.19[ab]	0.0042 ± 0.0003[a]	127.15 ± 2.48[a]	29.20 ± 0.24[a]	106.86 ± 1.13[a]
	P. alternifolium	12.95 ± 0.33[a]	0.0051 ± 0.0001[a]	94.05 ± 0.44[b]	28.21 ± 1.04[a]	101.28 ± 1.92[a]

capacities of *A. mangium* in response to elevated temperature are consistent with the findings of Yu and Ong (2002), who also reported that 30–32°C as the optimum temperature for photosynthetic CO_2 assimilation of *A. mangium* phyllodes. Le et al. (2016b) also reported enriched photosynthesis in terms of CO_2 assimilation rate for *A. auriculiformis* at elevated temperature compared to native heath species, *Andira inermis* and *Mangifera indica. Acacia mangium* appears well-adapted to higher temperatures and potentially high light intensity typical of a tropical climate likely due to its adaptation of their photosystem II (Le et al., 2019; Yu & Ong, 2002). This variation is also possible due to the balance between RuBP carboxylation and regeneration, which are both temperature-dependent processes of photosynthesis (Hikosaka et al., 1999, 2016).

For the four native heath species, we found that increasing temperature by 5°C lowered the photosynthetic capacities of secondary species (*C. inophyllum* and *P. alternifolium*) but did not affect the early secondary species (*B. arborescens* and *D. suffruticosa*). Our results may reflect light preference of secondary species as they are slow-growing and shade-tolerant species that are greatly adapted to low light levels (*i.e.* lower temperature) (Bloor & Grubb, 2003; Hashim et al., 2016; Poorter & Bongers, 2006; Slik, 2009). In contrast, early secondary species are light-demanding (Davies & Semui, 2006; Kartawinata et al., 2008; Slik, 2009) and their CO_2 assimilation and photosynthetic capacities do not seem to be affected by elevated temperature. Comparable findings were reported by Ribeiro et al. (2005) in Brazil, whereby an early secondary tree species, *Guazuma ulmifolia* had significantly higher net CO_2 assimilation than a secondary tree species, *Rhamnidium elaeocarpum* when exposed to high irradiance and temperature conditions. Based on their photosynthetic performances, there appears to be preliminary evidence from our study that the early secondary species are able to cope with the variations in environmental parameters, such as high light availability and temperature, in disturbed forest habitats as well as in the presence of invasive *A. mangium*, despite experiencing no improvement in their CO_2 assimilation rates.

Similar to Novriyanti et al. (2012), our study has also revealed that *A. mangium* at 25°C has lower A and E but higher WUE than native species, although it is crucial to note that the former study utilized indigenous Australian *Acacia* and *Eucalyptus* seedlings in a controlled ex-situ environment. Contrastingly, the increase in A of *A. mangium* at 30°C displayed greater E and G_s by two-fold but lower WUE than other heath species. Based on these findings, we suggest that differences in photosynthetic capacities between the study species (invasive *vs*. heath species) may be related to the stomatal control mechanisms that create a trade-off between CO_2 demands for photosynthesis and water loss via transpiration in response to varying environmental parameters (Lawson et al., 2010; Medina et al., 2002). At the same time, under optimum environmental conditions, biochemical processes in the mesophyll cells, which contribute to photosynthetic rate, are also improved due to increased enzymatic activity and electron transport chain capacity (Li et al., 2016). Different radiation quality has also been reported in influencing photosynthesis of *A. mangium*, where exposure to white light or complete spectrum of sunlight resulted in higher photosynthetic performances than monochromatic radiation (Yu & Ong, 2003) but this aspect was not determined in our study.

Additionally, higher A, E and G_s with lower WUE in *A. mangium* at elevated temperature could possibly be due to its rapid uptake of soil water compared to the different successional groups of heath forest species. Introduced fast-growing species, such as invasive *A. mangium*, can consume much more soil water than native species (Ibrahim, 2020; Siddiq & Cao, 2016). Several studies have also reported that *Acacia* species are able to modify soil water dynamics in field and controlled environments (Do et al., 2008; Dye & Jermain, 2004; Groengroeft et al., 2018; Le Maitre et al., 2000; Otieno et al., 2001, 2005). These findings can have important implications on water-limited and nutrient-poor forests, such as tropical heath forests, particularly with the continued presence of *Acacia* species. *Acacia* species are known to reduce soil nutrient and water availability (Ibrahim, 2020; Le Maitre et al., 2000; Norisada et al., 2005; Tanaka et al., 2015), thus negatively impacting the growth performance and productivity of native species in response to competition for water and nutrients.

No consistent pattern (*i.e.* lower or no differences) was reported for either the early secondary or secondary species in terms of their G_s, E and WUE responses to high temperature (30°C). In general, species with thicker leaf tissues and more compact leaves (*i.e.* high leaf mass area or LMA) can enhance water diffusional resistance, causing greater stomatal resistance (*i.e.* lower G_s) and transpirational resistance (*i.e.* lower E), thus reducing WUE and total photosynthetic output (Gibson, 1998; Givnish, 1988; Novriyanti et al., 2012). Yusoff (2015) showed that heath forest species have thicker leaves compared to pioneer species, while invasive *Acacia* species recorded similar or slightly lower LMA than heath forest species (Jaafar, 2020; Osunkoya et al., 2004), which typically possesses relatively small but scleromorphic leaves (Turner et al., 2000). The differences in leaf morphological traits may have resulted in higher A, E and G_s but lower WUE in *A. mangium* than native heath species at elevated temperature but these attributes cannot be further confirmed as leaf morphology was not assessed in this study.

Patterns for photosynthetic CO_2 response curves were similar to those of the photosynthetic light response curves at 25°C, such that the secondary species' response curves (particularly *P. alternifolium*) dominated higher photosynthetic capacities, followed by invasive *A. mangium* and early secondary species. At 400 ppm, secondary species displayed significantly higher A compared to early secondary species and invasive *A. mangium*. However, at elevated CO_2 (700 ppm), only the invasive *A. mangium* and *P. alternifolium* (secondary species) showed enhanced A by *c.a.* 64% and *c.a.* 22%, respectively, compared to ambient CO_2 level. Comparable to elevated temperature, the enhancement of A here was associated with increases in E and G_s but also lower WUE, however, this pattern was clearly seen for *P. alternifolium* only and not invasive *A. mangium*. Similar increases in photosynthetic capacities with elevated CO_2 have also been recorded in other invasive species, such as mesquite (*Prosopis glandulosa*) (Polley et al., 2003), *Bromus madritensis, Mikania micrantha, Wedelia trilobata* and *Ipomoea cairica* (Salo, 2005). An increment of 37% in photosynthetic capacities has been reported when *A. mangium* was treated with elevated CO_2 (354 *vs.* 712 ppm) (Ziska et al., 1991). The fast-growing trait of *Acacia* species could also be a factor in contributing toward higher above-ground productivity (Atkin et al., 1999) and potentially CO_2 assimilation at elevated CO_2.

For the native species in our study, elevated CO_2 appeared to increase photosynthetic capacity of secondary species (*P. alternifolium* only) but did not affect the early secondary species and *C. inophyllum* (secondary species). Many plant species increase their photosynthesis and growth under elevated CO_2 and unlimited environmental resources (Choi et al., 2017), although some reviews concluded that elevated CO_2 is unlikely to have any positive effect on tropical forest productivity (*e.g.*, Wright, 2005). We suggest that the discrepancies in A between species of different successional groups in our study may be due to between-species differences in leaf morphology and anatomy resulting in changes to light-harvesting process, CO_2 carboxylation (Rubisco production and activity) and leaf chemistry, such as N concentration (Choi et al., 2017; Niinemets, 2010; Novriyanti et al., 2012; Rogers et al., 1996). In a review of photosynthetic capacities of 43 different trees species, Niinemets (2010) concluded that light-harvesting process, which in turn promotes CO_2 diffusion into the mesophyll cell through the stomata resulting in higher photosynthetic capacities, was efficiently generated for species that are tall and large-sized with high foliage aggregation. Our secondary species (*P. alternifolium*) have thick and narrow leaves (*i.e.* high LMA) (Yusoff, 2015) compared to the early secondary species (*personal observation*), and this could have resulted in rapid light-harvesting process and CO_2 carboxylation in secondary species.

In terms of biochemical photosynthetic response curve parameters estimated using CO_2 response curves at 25°C and PPFD of 1500 μmol (photon) m^{-2} s^{-1}, the increases in A_{max} by *P. alternifolium* (secondary heath forest species) and invasive *A. mangium*, but not early secondary species, were associated with patterns of decreasing LCP and J. This study also revealed that the RuBP carboxylation efficiency and quantum yield did not have much influence on A_{max}. This was similarly observed by Hikosaka et al. (1999) where photosynthetic rate of plants grown below 30°C was limited by RuBP regeneration, and not RuBP carboxylation. In addition, plants with a lower LCP tolerate deeper shade and lower light level than plants with a higher LCP (Valladares & Niinemets, 2008), which is consistent with *P. alternifolium* as a slow-growing, shade-tolerant and secondary plant species (Hashim et al., 2016; Osunkoya et al., 2005) but not with *A. mangium*. However, our study also seemed to suggest that invasive *A. mangium* can express remarkable adaptability to a wide spectrum of light conditions (*i.e.* shade-tolerant traits and light-demanding traits) and thus have the ability to rapidly regenerate under both forest canopy and gaps in the forest communities. Similar findings were also previously reported by Aguilera et al. (2015), Badalamenti et al. (2018), Bonari et al. (2017), and Rodríguez et al. (2017) that in addition to high-light adaptation, invasive *Acacia dealbata* and *A. saligna* demonstrated shade-tolerant traits under the canopy of native and non-native Mediterranean forest ecosystems of South America and Europe.

One main limitation of our study was the use of only two specific values of elevated temperature (30°C) and CO_2 concentrations (700 ppm), rather than a range of values. In particular, the elevated temperature of 30°C was likely more similar to on-site daily temperatures (mean in-situ leaf temperatures ranged from 26.5°C to 29.0°C), rather than as a way of simulating a potential global warming scenario in a tropical climate. For example, maximum daily temperatures for Brunei Darussalam can reach 31–35°C (Brunei Darussalam Meteorological Department, *unpublished data*). Other photosynthesis studies on *A. mangium* have attempted higher temperatures of between 30°C and 40°C (Le et al., 2019; Yu & Ong, 2002), while optimum ecosystem air temperature for photosynthesis recorded in seven tropical forest sites ranged from 23.7°C to 28.1°C (Tan et al., 2017). Additionally, our study's interpretation is limited by our approach of quantifying photosynthetic data using instantaneous gas exchange parameters through in-situ leaf measurements, as leaf-level responses are difficult to scale up to whole plant or ecosystem-level responses. Nevertheless, we highlight that our findings at leaf-level are important in providing preliminary evidence that invasive *A. mangium* appears to have an advantage in photosynthetic responses over co-occurring native species in response to elevated temperature (30°C) and CO_2 (700 ppm). Further studies are necessary to provide a more complete model of photosynthetic responses, including biochemical responses with leaf morphological and anatomical traits, of invasive alien and native species in response to long-term exposure and combined effects of changing temperature, CO_2 concentrations, rainfall levels, and nutrients.

Our findings have broader implications upon sustainable forestry practices and the management of invaded tropical forests. Firstly, we found that photosynthetic responses of early secondary species (*B. arborescens* and *D. suffruticosa*) co-existing with *A. mangium* appear to be relatively unaffected by changes in temperature and CO_2 concentrations. This suggests that while *A. mangium* may continue to invade these coastal heath forests, the early secondary species (*B. arborescens* and *D. suffruticosa*) may be suitable species to use for restoration of *Acacia*-invaded coastal heath habitats as their photosynthetic responses remained unaffected and they are able to co-occur with *Acacia mangium*. Secondly, forest restoration programs are increasingly implemented worldwide as a climate change mitigation strategy (Bastin et al., 2019; Chazdon & Brancalion, 2019), with some programs opting to use fast-growing non-native species such as *Acacia*. Our results indicate that non-native invasive species may positively benefit from the impacts of climate change to the detriment of native flora, and thus non-natives should be avoided in these forest restoration programs. Lastly, our findings are also important for policymakers to consider in developing effective invasive species management strategies, as invasive species ranges are anticipated to further expand under climate change scenarios predicted by the Intergovernmental Panel for Climate Change [IPCC] (2014, 2018). At our study sites in tropical Brunei Darussalam, if *Acacia* invasion into these invaded heath forests is left unmanaged, then the resulting monodominance of *Acacia* species (Osunkoya & Damit, 2005) may eventually cause further ecosystem changes which will likely be enhanced by the effects of climate change.

Data deposition

Data on leaf gas exchange and biochemical parameters of photosynthesis of invasive *Acacia mangium* and tropical heath forest species are available at Dryad Digital Repository (https://doi.org/10.5061/dryad.d51c5b00d).

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