ECOPHYSIOLOGICAL RESPONSES OF MISTLETOE *DENDROPHTHOE CURVATA* (LORANTHACEAE) TO VARYING ENVIRONMENTAL PARAMETERS

QV Le[1, 2], KU Tennakoon[1, *], F Metali[1], LBL Lim[3] & JF Bolin[4]

[1]*Faculty of Science and Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Tungku Link, Gadong, BE 1410, Brunei Darussalam*
[2]*Faculty of Biology, Vinh University, 182 Le Duan, Vinh City, Nghe An Province, Vietnam*
[3]*Faculty of Science, Universiti Brunei Darussalam, Tungku Link, Gadong, BE 1410, Brunei Darussalam*
[4]*Department of Biology, Catawba College, 2300 W Innes St Salisbury, NC, 28144, USA*

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LE QV, TENNAKOON KU, METALI F, LIM LBL & BOLIN JF. 2016. Ecophysiological responses of mistletoe *Dendrophthoe curvata* (Loranthaceae) to varying environmental parameters. We measured parameters of photosynthetic capacity, instantaneous gas exchange and leaf mineral contents of tropical mistletoe *Dendrophthoe curvata* parasitising three hosts, viz, *Andira inermis* (Fabaceae), *Mangifera indica* (Anacardiaceae) and *Vitex pinnata* (Verbenaceae) in a secondary tropical heath (*Kerangas*) forest patch in Brunei Darussalam in response to changes in light intensity, leaf temperature and atmospheric CO_2 concentrations. The response patterns of maximum photosynthesis, maximum carboxylation rate of rubisco, electron transport rate for ribulose-1,5-bisphosphate regeneration and CO_2 assimilation rate of *D. curvata* revealed that its photosynthesis was co-limited by both light and temperature and did not saturate at natural CO_2 concentrations (380 ppm). The effects of CO_2 elevation on *D. curvata* photosynthesis was long term due to the partial dependence of obligate hemiparasitic mistletoe on host-derived carbon. Stomatal conductance of *D. curvata* was moderately sensitive to CO_2 elevation under the natural conditions that the measurements were made. Notably, ecophysiological responses of *D. curvata* including potential photosynthesis, gas exchange parameters and leaf mineral profiles were significantly different when the mistletoe parasitised three different host species.

Keywords: Abiotic factor, host specificity, mistletoe resilience, quantitative photosynthesis

INTRODUCTION

Mistletoes are aerial hemiparasitic plants that connect to vascular tissues of host stem for water and nutrients (Mathiasen et al. 2008). Mistletoes are usually reported as having lower photosynthetic capacity, higher transpiration rate and less sensitivity of stomata to water deficit than the associated hosts (Glatzel & Geils 2009). In fact, mistletoes have the lowest photosynthetic capacity among C_3 plants (Stewart & Press 1990) as well as low electron transport rates and low Hill reaction activities in thylakoids. Thus, they behave like shade plants (Johnson & Choinski 1993, Strong et al. 2000).

Mistletoes show no significant differences in photosynthetic rates compared with associated hosts (Marshall et al. 1994, Lüttge et al. 1998) and exhibit lower transpiration rate under low water status (Küppers 1992, Küppers et al. 1992) or high salinity (Chen et al. 2013). Recently, we demonstrated that mistletoes synchronised light-saturated photosynthesis and transpiration rates according to the host species that they are associated with and the host-specific responses might drive the intraspecific variations in mistletoe physiology (Le et al. 2014). These findings demonstrated that mistletoes could adjust many physiological processes to acclimatise to different habitat conditions. However, it is still unclear how mistletoes make these ecophysiological modifications in response to varying environments, in particular towards fluctuation of environmental factors related to climate change such as temperature, light intensity and CO_2 concentrations.

**kushan.tennakoon@ubd.edu.bn*

In this study, we investigated how a tropical mistletoe, *Dendrophthoe curvata*, adjusted its ecophysiological performances in response to changes in environmental factors and how those responses were regulated by different hosts that it depended on for water and nutrition. To address these issues, we evaluated the ecophysiological responses of *D. curvata* parasitising three host species (*Andira inermis*, *Mangifera indica* and *Vitex pinnata*) under varying light, temperature and CO_2 regimes in a natural habitat, i.e. secondary tropical heath (*Kerangas*) forest, found in areas with nutrient-poor and sandy soils in Brunei Darussalam.

MATERIALS AND METHODS

Study site and species

This study was conducted using three hemiparasitic mistletoe *D. curvata*–host associations, namely, *D. curvata–A. inermis*, *D. curvata–M. indica* and *D. curvata–V. pinnata*. The in-situ investigations were carried out from June 2013 till September 2013 in a patch of secondary *Kerangas* forest in the Brunei-Muara district, Brunei Darussalam (4° 58' N, 114° 58' E).

Gas exchange measurements

Six replicates per mistletoe–host association were randomly selected for gas exchange measurements. For each replicate, one healthy mistletoe leaf, which was fully expanded and exposed to sunlight (collected from the top of the tree canopy), was sampled as described by Chen et al. (2013) and Le et al. (2014). Gas exchange was measured on detached leaves as described by Yan and Wang (2011). Leaf gas exchange measurement, based on the method described by Johnson and Murchie (2011), was carried out using portable gas exchange system fitted with 2 cm × 3 cm chamber. An LED lamp was used as light source. Relative humidity inside the chamber was kept at 50–60% and flow rate of gas into the chamber was maintained at 500 µmol s^{-1}. Prior to each measurement, the leaf was clamped into the chamber and left to stabilise to the measuring conditions (15–30 min) until CO_2 assimilation rate and stomatal conductance values were steady. Four paired light–temperature treatments of two photosynthetically active radiation levels (500 and 1500 µmol photon m^{-2} s^{-1}) and two leaf temperatures (25 and 30 °C) were used to measure CO_2 response curves. These were assigned as: treatment I (500 µmol photon m^{-2} s^{-1} and 25 °C), treatment II (1500 µmol photon m^{-2} s^{-1} and 25 °C), treatment III (500 µmol photon m^{-2} s^{-1} and 30 °C) and treatment IV (1500 µmol photon m^{-2} s^{-1} and 30 °C). Two levels of photosynthetically active radiation (500 and 1500 µmol photon m^{-2} s^{-1}) were applied to represent light intensity at mid-canopy and top-canopy respectively. Leaf temperatures of 25 and 30 °C represented mean low and high daytime temperatures experienced in tropical heath forests of Brunei Darussalam (Dykes 2000). Response curves of CO_2 assimilation rates (A) to intercellular CO_2 concentrations (C_i) were generated with varying air CO_2 concentrations (C_a) in the chamber, namely, 50, 100, 150, 250, 380, 500, 700, 950 and 1250 ppm. Carbon dioxide assimilation rates (A) (µmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s) (mol H_2O m^{-2} s^{-1}) and transpiration rates (E) (mmol H_2O m^{-2} s^{-1}) were recorded directly from the portable gas exchange system. Water-use efficiency (WUE) (µmol CO_2 mmol H_2O^{-1}) was calculated by A/E ratio as described by Farquhar and Richards (1984). Maximum photosynthesis (A_{max}) (µmol CO_2 m^{-2} s^{-1}) was generated by fitting A–C_i curves into a Mitscherlich model (Peek et al. 2002) using R software (2013) as follows:

$$Y = \alpha\ (1 - e^{-\beta(X - \delta)})$$

where Y = instantaneous CO_2 assimilation rate (µmol CO_2 m^{-2} s^{-1}), X = intercellular CO_2 concentration (ppm), α = maximum photosynthesis (µmol CO_2 m^{-2} s^{-1}), β = curve slope and δ = apparent CO_2 compensation point (ppm).

Maximum carboxylation rate of rubisco (V_{cmax}) (µmol CO_2 m^{-2} s^{-1}) and potential electron transport rate for regeneration of ribulose-1,5-bisphosphate (J) (µmol CO_2 m^{-2} s^{-1}) were generated by fitting A–C_i curves into Faquhar–Von Caemmerer–Berry biochemical model of photosynthesis (Farquhar et al. 1980, Farquhar & Von Caemmerer 1982, Von Caemmerer 2000) following the procedure described by Sharkey et al. (2007).

Mineral analysis

For each of the three mistletoe–host associations, three healthy and fully expanded leaves of the mistletoe from each of six host individuals with parasitising mistletoes were sampled as described by Tennakoon et al. (2011, 2014). Leaves were rinsed with distilled water and oven dried at 70 °C for 2 days until constant weight was achieved. Leaves of mistletoe from the same associations were bulked and then subdivided into three replicates.

Dried leaf samples (1 g) were ground and digested using 10 mL of concentrated sulphuric acid (H_2SO_4). Total N and P contents were analysed according to methods modified from Metali et al. (2014) and measured using flow injector analyser. For total K, Ca and Mg analysis, 0.5 g dried leaves was digested completely with 5 mL concentrated hydrochloric acid (HCl) and 0.5 mL concentrated nitric acid (HNO_3) using microwave digestion system (Metali et al. 2014). Total K, Ca and Mg concentrations were determined using flame atomic absorption spectrophotometry.

Statistical analysis

Analysis of variance (one-way ANOVA, multi-way ANOVA), post-hoc Tukey test (Tukey HSD) and Student *t*-test were conducted at 5% significant level in R version 3.0.1 (2013).

RESULTS

Photosynthetic parameters (A_{max}, V_{cmax} and J) of *D. curvata* parasitising three host species under different regimes of light and temperature

We first plotted A of *D. curvata* versus C_i to generate photosynthetic CO_2 response (A–C_i) curves (Figure 1). The fitting parameters (A_{max}, V_{cmax} and J) of these A–C_i curves are summarised in Table 1. Multi-way ANOVA results presented in Table 2 showed that all environmental factors investigated in this study (photosynthetically active radiation, leaf temperature and host species) had significant effects on photosynthetic parameters of *D. curvata* ($p < 0.001$). The increment of photosynthetically active radiation (from 500 to 1500 µmol photon m^{-2} s^{-1}) significantly increased A_{max}, V_{cmax} and J of *D. curvata* measured at 25 °C (*t*-test, $p < 0.05$, < 0.01 and < 0.01 respectively) but not at 30 °C (*t*-test, $p > 0.05$). The increment of leaf temperature (from 25 to 30 °C) significantly increased A_{max}, V_{cmax} and J of *D. curvata* measured at 500 µmol photon m^{-2} s^{-1} (*t*-test, $p < 0.05$, < 0.01 and < 0.05 respectively) and only significantly increased V_{cmax} at 1500 µmol photon m^{-2} s^{-1} (*t*-test, $p < 0.05$).

The mistletoe *D. curvata* exhibited significant differences in A_{max}, V_{cmax} and J when parasitising three different host species (*A. inermis*, *M. indica* and *V. pinnata*) under all four paired light–temperature treatments investigated in this study (Tables 1 and 2). *Dendrophthoe curvata* parasitising *V. pinnata* exhibited significantly higher overall A_{max}, V_{cmax} and J compared with that parasitising *A. inermis* or *M. indica* (ANOVA, $p < 0.05$).

Instantaneous gas exchange parameters (A, g_s, E and WUE) of *D. curvata* parasitising three host species under different regimes of air CO_2 concentration

We used data measured at treatment IV (1500 µmol photon m^{-2} s^{-1} and 30 °C), in which *D. curvata* exhibited higher A_{max}, V_{cmax} and J than other treatments, to investigate the effects of different C_a levels to variations of A, g_s, E and WUE of *D. curvata* (Table 3). The elevation of C_a (from 380 to 500 ppm) significantly induced an increase in A and WUE (*t*-test, $p < 0.01$) but not in g_s and E of *D. curvata* (*t*-test, $p > 0.05$). *Dendrophthoe curvata* parasitising different host species (*A. inermis*, *M. indica* and *V. pinnata*) exhibited significant differences in A, g_s, E and WUE at both C_a of 380 and 500 ppm (ANOVA, $p < 0.05$). At these levels of C_a (i.e. 380 and 500 ppm), *D. curvata* parasitising *V. pinnata* exhibited significantly higher A and WUE but significantly lower g_s and E compared with that parasitising the other two host species. *Dendrophthoe curvata* parasitising different host species exhibited different magnitudes of A and WUE increments induced by CO_2 elevation with significantly higher incremental magnitudes of A and WUE in *D. curvata* parasitising *V. pinnata* (ANOVA, $p < 0.05$).

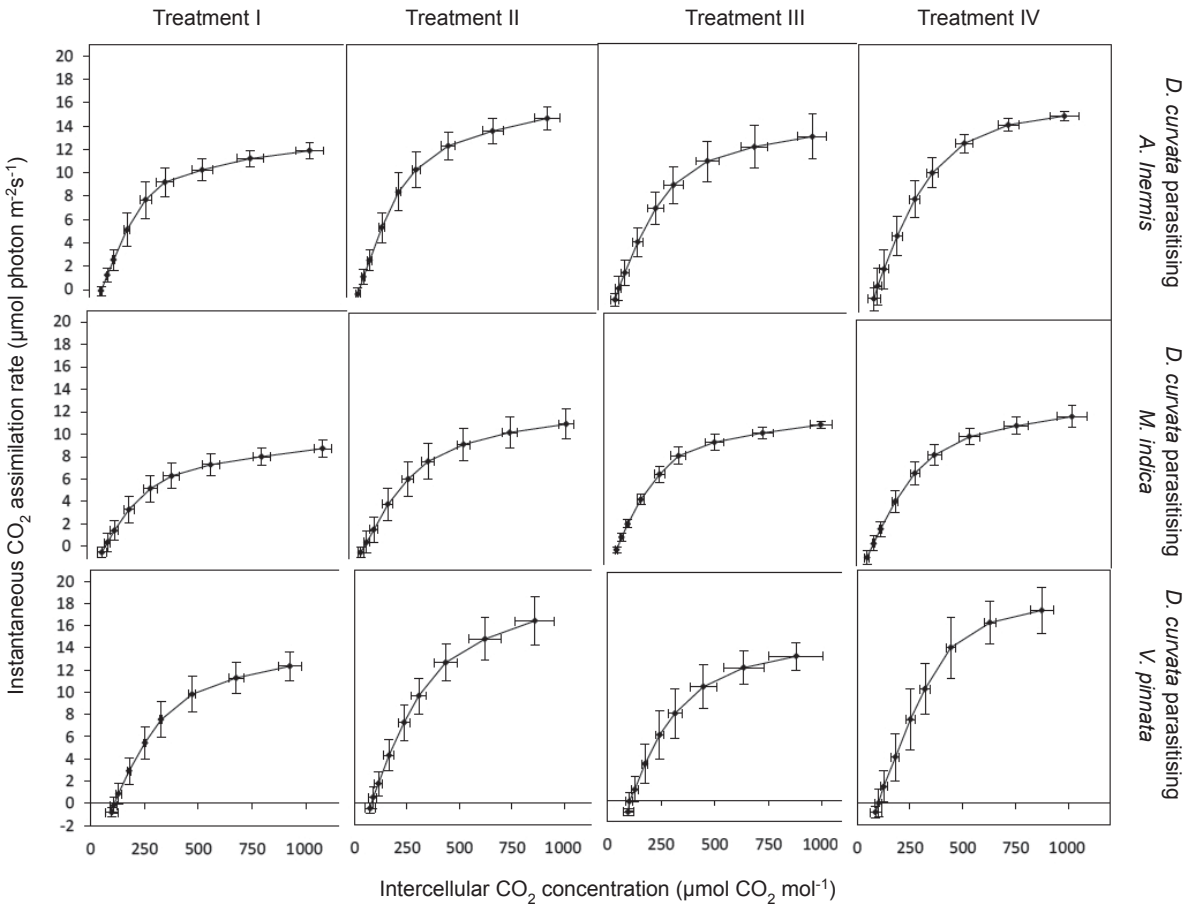

Figure 1 Photosynthetic CO_2 response curves of *Dendrophthoe curvata* parasitising three host species (*Andira inermis*, *Mangifera indica* and *Vitex pinnata*) under different regimes of light and temperature; treatment I: 500 µmol photon m^{-2} s^{-1} and 25 °C, treatment II: 1500 µmol photon m^{-2} s^{-1} and 25 °C, treatment III: 500 µmol photon m^{-2} s^{-1} and 30 °C, treatment IV: 1500 µmol photon m^{-2} s^{-1} and 30 °C; data are expressed as means ± standard deviations (n = 6)

Variations of mineral profiles in *D. curvata* parasitising different host species

Dendrophthoe curvata parasitising different host species (*A. inermis*, *M. indica* and *V. pinnata*) exhibited significant differences in leaf N, P, K, Ca and Mg contents (ANOVA, $p < 0.001$, Table 4). *Dendrophthoe curvata* parasitising *V. pinnata* had significantly higher leaf N, P and K contents and that parasitising *M. indica* showed significantly higher leaf Ca and Mg contents compared with *D. curvata* parasitising *A. inermis* or *V. pinnata* (ANOVA, $p < 0.001$).

DISCUSSION

This study aimed at understanding the resilience of tropical mistletoes. Here, we examined variations of photosynthetic parameters, instantaneous gas exchange performance and mineral profiles in leaves of *D. curvata* parasitising three host species (*A. inermis*, *M. indica* and *V. pinnata*) under different combined regimes of light intensity, temperature and CO_2 concentration and investigated how ecophysiological responses of the mistletoe vary based on the particular hosts it utilised.

The variations of $A–C_i$ curves, photosynthetic capacity (in relation to A_{max}, V_{cmax} and J) of *D. curvata* to different levels of light and temperature as well as instantaneous CO_2 assimilation rates of *D. curvata* in response to CO_2 elevation manipulated in this study reflected the photosynthetic flexibility of this hemiparasite. Varying patterns of photosynthetic parameters of *D. curvata* in response to changes of light

Table 1 Photosynthetic parameters of *Dendrophthoe curvata* parasitising three different host species (*Andira inermis*, *Mangifera indica* and *Vitex pinnata*) under different regimes of light and temperature

D. curvata trait	Mistletoe parasitising host		Treatment			
			500 µmol photon m^{-2} s^{-1} and 25 °C	1500 µmol photon m^{-2} s^{-1} and 25 °C	500 µmol photon m^{-2} s^{-1} and 30 °C	1500 µmol photon m^{-2} s^{-1} and 30 °C
A_{max} (µmol CO_2 m^{-2} s^{-1})	*D. curvata* parasitising *A. inermis*		11.8 ± 0.6 b	14.9 ± 0.9 b	13.3 ± 1.8 b	15.8 ± 0.8 b
	D. curvata parasitising *M. indica*		8.6 ± 0.5 a	11.4 ± 1.1 a	10.9 ± 0.2 a	12.8 ± 1.0 a
	D. curvata parasitising *V. pinnata*		12.9 ± 1.1 c	17.8 ± 2.5 c	14.3 ± 1.2 c	20.1 ± 1.4 c
	Overall (n = 3)		11.1 ± 2.2	14.7 ± 3.2	12.8 ± 1.8	16.2 ± 3.7
	ANOVA	F-value	50.5	23.5	11.5	64.1
		p-value	< 0.001	< 0.001	< 0.001	< 0.001
V_{cmax} (µmol CO_2 m^{-2} s^{-1})	*D. curvata* parasitising *A. inermis*		38.0 ± 2.5 b	42.7 ± 4.7 b	48.3 ± 8.3 ab	54.6 ± 2.6 ab
	D. curvata parasitising *M. indica*		28.2 ± 2.7 a	33.4 ± 3.3 a	41.1 ± 5.7 a	43.3 ± 6.7 a
	D. curvata parasitising *V. pinnata*		39.3 ± 5.0 c	45.1 ± 6.2 c	52.2 ± 6.9 b	64.9 ± 14.6 b
	Overall (n = 3)		35.2 ± 6.1	40.4 ± 6.2	47.2 ± 5.6	54.3 ± 10.8
	ANOVA	F-value	17.1	9.6	3.9	7.9
		p-value	< 0.001	< 0.01	< 0.05	< 0.01
J (µmol CO_2 m^{-2} s^{-1})	*D. curvata* parasitising *A. inermis*		57.1 ± 3.4 b	70.5 ± 4.5 b	65.5 ± 8.0 b	77.1 ± 9.0 b
	D. curvata parasitising *M. indica*		44.2 ± 4.5 a	55.3 ± 6.1 a	51.0 ± 6.1 a	56.5 ± 4.7 a
	D. curvata parasitising *V. pinnata*		71.4 ± 5.1 c	85.6 ± 13.3 c	75.0 ± 8.7 b	98.3 ± 11.2 c
	Overall (n = 3)		57.6 ± 13.6	70.5 ± 15.1	63.8 ± 12.1	77.3 ± 20.9
	ANOVA	F-value	57.4	17.5	15.1	34.1
		p-value	< 0.001	< 0.001	< 0.001	< 0.001

n = 6, data are expressed as means ± standard deviations, different letters indicate differences of means at $p < 0.05$; A_{max} = maximum photosynthesis, V_{cmax} = maximum carboxylation rate of rubisco, J = potential electron transport rate for the regeneration of ribulose-1,5-bisphosphate

and temperature levels indicated that *D. curvata* photosynthesis is co-limited by both light and temperature under paired light–temperature condition of 500 µmol photon m^{-2} s^{-1} and 25 °C. However, photosynthetic parameters (A_{max}, V_{cmax} and J) of *D. curvata* are variously dependent on environmental factors (light and temperature) investigated in this study. This agrees with reports that V_{cmax} and J of C_3 plants respond differently to various leaf temperatures and V_{cmax} has higher optimal temperature than J (Farquhar et al. 1980, Leuning 1997, Lin et al. 2013). Our results also showed that light intensity affected V_{cmax} and J of the tropical mistletoe differently and modulated the temperature dependent patterns of V_{cmax} and J. At photosynthetically active radiation of 1500 µmol photon m^{-2} s^{-1}, the increment of temperature from 25 to 30 °C induced significant increase of V_{cmax} but did not contribute in the increment of A_{max}. Thus, the photosynthetic capacity of *D. curvata* is limited only by J at this light intensity level. This finding is in agreement with the study by Strong et al. (2000), in which temperate mistletoes limit their photosynthetic capacity by behaving like shade plants with low electron

Table 2 Multi-way ANOVA of photosynthetically active radiation, leaf temperature and host species to maximum photosynthesis (A_{max}), maximum carboxylation rate of rubisco (V_{cmax}) and potential electron transport rate (J) of *Dendrophthoe curvata*

Parameter	Degree of freedom	A_{max}		V_{cmax}		J	
		F value	p value	F value	p value	F value	p value
Photosynthetically active radiation	1	143.1	< 0.001	15.6	< 0.001	53.8	< 0.001
Temperature	1	30.0	< 0.001	69.0	< 0.001	13.2	< 0.001
Host	2	112.9	< 0.001	27.6	< 0.001	97.8	< 0.001
Light × Temperature	1	0.2	0.67	0.3	0.56	0.0	0.87
Light × Host	2	10.7	< 0.001	1.1	0.34	2.8	0.06
Temperature × Host	2	0.5	0.63	1.2	0.31	0.5	0.60
Light × Temperature × Host	2	0.8	0.45	0.8	0.44	1.5	0.23
Residual	60						

transport rates. The best light intensity and temperature required for optimal photosynthesis of *D. curvata* growing in the tropical regions are above 500 µmol photon m^{-2} s^{-1} and 25 °C and not exceeding 1500 µmol photon m^{-2} s^{-1} and 30 °C respectively. However, further investigations are required over multiple seasons to find definitive answers for questions of this nature.

In this study, instantaneous CO_2 assimilation rates of *D. curvata* significantly increased with elevation of air CO_2 concentrations (from 380 to 500 ppm). A number of studies have also reported that C_3 plant photosynthesis increases with increment of ambient CO_2 concentration (Ainsworth & Rogers 2007, Barnaby & Ziska 2012). Instantaneous CO_2 assimilation rates increase upon sudden exposure to elevated CO_2 and then become down-regulated when acclimating to higher ambient CO_2 levels because of source/sink balance (Drake et al. 1997). However, evidence from free air concentration enrichment experiments (Leakey et al. 2012) suggested that the enhancement of photosynthesis induced by elevated CO_2 concentration is sustained over time. In addition, most mistletoes partially depend on carbon derived from associated hosts (Popp & Richter 1998), thus, it may be reasonable for *D. curvata* to more aptly sustain its increased photosynthesis in response to CO_2 even during long-term exposure to elevated CO_2 concentration when compared with autotrophic plants. Furthermore, one of the most consistent and species-specific responses of plants to elevated ambient CO_2 concentrations is to reduce stomatal conductance and consequently down-regulate photosynthesis (Hetherington & Woodward 2003, Ainsworth & Long 2005). However, we found that g_s of *D. curvata* did not change significantly with progressive elevation of CO_2 concentrations (from 380 to 500 ppm). Thus, we excluded the possibility of photosynthesis down-regulation by *D. curvata* induced by stomatal closure when exposed to long-term elevated CO_2 concentrations. This moderate sensitivity of stomata to CO_2 elevation was also reported in the root hemiparasitic Orobanchaceae (Phoenix & Press 2005), *Striga hermonthica* and *S. asiatica* (Watling & Press 1997). Therefore, our finding is not an exceptional case for angiosperm hemiparasites.

Due to the complete dependence of *D. curvata* as mistletoe on hosts for minerals and water, the latter influences the performance of the former via modification of physiological and biochemical processes (Glatzel & Geils 2009). Our findings have revealed that all potential photosynthetic parameters (A_{max}, V_{cmax} and J), instantaneous gas exchange readings (A, g_s, E and WUE) measured at top-canopy light level and 30 °C (the condition in which potential photosynthesis reached maximal capacity) and leaf mineral profiles (N, P, K, Ca and Mg) of *D. curvata* were significantly influenced by the nature of host species and not exclusively due to ambient variations of sunlight, temperature and CO_2. The intraspecific variations of mineral profiles of *D. curvata* parasitising different host

Table 3 Instantaneous gas exchange parameters of *Dendrophthoe curvata* parasitising different host species (*Andira inermis*, *Mangifera indica* and *Vitex pinnata*) measured at 1500 µmol photon m^{-2} s^{-1}, 30 °C and under two air CO_2 (C_a) concentrations (380 and 500 ppm)

C_a (ppm)	Mistletoe parasitising host		A (µmol CO_2 m^{-2} s^{-1})	g_s (mol H_2O m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	WUE (µmol CO_2 mmol H_2O^{-1})
380	*D. curvata* parasitising *A. inermis*		8.0 ± 1.6 ab	0.16 ± 0.03 b	2.6 ± 0.4 b	3.1 ± 0.7 a
	D. curvata parasitising *M. indica*		7.1 ± 0.7 a	0.17 ± 0.04 b	2.8 ± 0.7 b	2.7 ± 0.7 a
	D. curvata parasitising *V. pinnata*		9.3 ± 1.5 b	0.10 ± 0.02 a	1.7 ± 0.2 a	4.8 ± 1.3 b
	Overall (n = 3)		8.2 ± 1.1	0.14 ± 0.04	2.4 ± 0.6	3.5 ± 1.1
	ANOVA	F-value	4.2	10.4	8.4	8.3
		p-value	< 0.05	< 0.01	< 0.01	< 0.01
500	*D. curvata* parasitising *A. inermis*		10.2 ± 1.3 ab	0.16 ± 0.03 b	2.7 ± 0.3 b	4.1 ± 0.8 a
	D. curvata parasitising *M. indica*		9.1 ± 0.9 a	0.15 ± 0.05 ab	2.7 ± 0.3 b	3.5 ± 0.9 a
	D. curvata parasitising *V. pinnata*		12.3 ± 2.0 b	0.10 ± 0.02 a	1.8 ± 0.3 a	6.5 ± 1.8 b
	Overall (n = 3)		10.5 ± 1.6 *	0.14 ± 0.03 *ns*	2.4 ± 0.5 *ns*	4.7 ± 1.5 *
	ANOVA	F-value	7.5	4.7	17.8	9.1
		p-value	< 0.01	< 0.05	< 0.001	< 0.01
			Δ A (%)	Δ g_s (%)	Δ E (%)	Δ WUE (%)
Δ	*D. curvata* parasitising *A. inermis*		29.7 ± 10.0 ab	-3.5 ± 1.4 a	-3.0 ± 1.3 a	33.8 ± 10.5 ab
	D. curvata parasitising *M. indica*		21.9 ± 5.7 a	-2.6 ± 1.8 a	-2.3 ± 1.7 a	23.9 ± 4.9 a
	D. curvata parasitising *V. pinnata*		36.1 ± 7.1 b	-4.5 ± 1.8 a	-3.4 ± 1.8 a	38.6 ± 8.3 b
	ANOVA	F-value	4.9	0.7	0.2	4.9
		p-value	< 0.05	0.49	0.80	< 0.05

n = 6, data are expressed as means ± standard deviations, different letters indicate differences of means at $p < 0.05$, overall comparison between two C_a concentrations using Student *t*-test, ns = not significant, * = $p < 0.05$; A = CO_2 assimilation rate, g_s = stomatal conductance, E = transpiration rate, WUE = water-use efficiency, Δ = per cent difference

species reported here provide new perspectives of the regulatory roles played by different hosts on the performance of mistletoes. Increased resource uptake by host trees increases resource partitioning to mistletoes, thus, enhancing shoot growth in mistletoes (Bickford et al. 2005). Host-specific influence (aluminium and non-aluminium accumulating host species) on mineral profiles of *D. curvata* has been reported by Scalon et al. (2013). These investigations support our hypothesis that mistletoe performance is regulated by the physiological conditions of different hosts.

Our study provides evidence that *D. curvata* photosynthesis is stimulated by increments of light intensity, temperature and ambient CO_2 concentrations in-situ. Unlike other studies, it provided quantitative responses of photosynthetic parameters under varying light, temperature and CO_2 levels for a tropical mistletoe associating with different hosts under the same microhabitat conditions. One limitation in our study was the interpretation of *D. curvata* performance using instantaneous gas exchange parameters and in-situ environmental data using leaves. One can debate that the response patterns

Table 4 Mean total leaf mineral concentrations of *Dendrophthoe curvata* parasitising different host species (*Andira inermis*, *Mangifera indica* and *Vitex pinnata*)

Mistletoe parasitising host		N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})
D. curvata parasitising *A. inermis*		4.46 ± 0.12 b	0.09 ± 0.05 a	6.93 ± 0.02 b	0.61 ± 0.00 a	1.27 ± 0.11 b
D. curvata parasitising *M. indica*		3.02 ± 0.10 a	0.34 ± 0.07 b	6.80 ± 0.03 a	3.69 ± 0.01 c	1.75 ± 0.18 c
D. curvata parasitising *V. pinnata*		7.58 ± 0.07 c	0.98 ± 0.08 c	9.56 ± 0.02 c	1.37 ± 0.00 b	0.91 ± 0.09 a
	F-value	1642.1	142.69	11,935	173,655	30.56
ANOVA	p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

n = 3, data are expressed as means ± standard deviations, different letters indicate differences of means at $p < 0.05$; N = nitrogen, P = phosphorus, K = potassium, Ca = calcium, Mg= magnesium

of a whole plant, or even a plant population, can be different. As acclimation is an intrinsic characteristic of any living organisms including mistletoe, under long-term exposure to changes of environmental parameters (light, temperature and CO_2), the magnitude of overall responses can be different (Leakey et al. 2009, Lin et al. 2012). Regardless of these limitations, here we conclusively showed that photosynthetic parameters of tropical mistletoe were strongly influenced by the specific host utilised.

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