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Photosynthetic abilities, light response, and stomatal function in six agroforestry species, *Dipterocarpus tuberculatus*, *D. alatus*, *Eucalyptus camaldulensis*, *Hevea brasiliensis*, *Colocasia gigantea*, and *C. esculenta* in responses to water deficit

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ABSTRACT: We investigated the physiological and morphological responses in six agroforestry tree species *Dipterocarpus tuberculatus*, *D. alatus*, *Eucalyptus camaldulensis*, *Hevea brasiliensis*, *Colocasia gigantea*, *C. esculenta* under limited water availability. Withholding water resulted in reduced field capacity by 71%, 86%, and 48% in *D. alatus*, *D. tuberculatus*, and *E. camaldulensis*, respectively, resulting in wilting, leaf chlorosis, and leaf burn, respectively. Stomatal density varied among the plant species (1.4–6.2 stomata per 0.0625 mm^2) and was unaffected by water regimes, whereas stomatal conductance (g_s), transpiration rate (E), and water use efficiency were reduced when plants were subjected to water deficit conditions. Generally, intracellular CO_2 of well-watered plants was not always maintained across increasing light intensity flux (PAR_i), although for *E. camaldulensis* this was not the case, as both well-watered and water deficit groups showed a reduction with increasing PAR_i. Net photosynthetic rate was significantly increased in well-watered plants as compared to water stressed plants, depending on the degree of PAR_i. In addition, a positive relation between g_s and E in each plant was demonstrated.

KEYWORDS: drought situation, photosynthetic photon flux, evapotranspiration rate, water efficiency

INTRODUCTION

Agroforestry is an initiative for promoting environmental rehabilitation in domestic community through the integrated management of trees rather than mono-plantations[1,2]. A sustainable land use system, intercropping forest trees, and agricultural/horticultural crops is a challenge. It can help in sequestration of atmospheric carbon into the soil[2], supplementing food products[3], improving their nutritional status[4], increasing the density of soil arbuscular mycorrhizal fungi[5], elevating crop productivity[6], and thus providing increased yield, food security, and economic income[7]. The physiological and morphological responses, specifically photosynthesis and biomass production, in millet (cereal crop), taro (storage root crop) and baobab (forest tree) intercropping system have been well established, allowing the coexistence of canopy and understorey plant species despite competitive shading for better biomass production[6]. Shading and water availability in the root zones influence the biomass production, and are considered as the major factors in controlling the agroforestry system[8–10]. Hence the light response curve of plant species under water limitation plays a key factor in agroforestry management and needs to be investigated.

Global warming and climate change have resulted in increased drought stress and is currently a matter of concern[11]. In deciduous agroforests, water constraint in the dry season is evidently found in each year. Stomatal function under water deficit conditions that prevent the water loss via stomatal closure has been investigated. In contrast, it limits the CO_2 assimilation and plant growth[12,13]. Drought sensitivity in higher plants depends on the degree of water limitation, plant species, drought exposure periods, their interactions, etc[14,15]. Plant species show individual responses to water-deficit stress as mentioned in large number of previous publications. Hence the basic knowledge on physiological, morphological and anatomical characters in plant responses to water shortage, especially in the summer and winter season, especially in agroforest tree species are restricted. Stomatal density in olive cultivars increases whereas the stomatal size is reduced, relating to drought stress (−1.5 MPa soil water potential) for 7 months[16]. Stomatal conductance is one of the most important parameters to identify the stomata closure, which is very sensitive to drought conditions[17]. The stomatal function in dynamic process of CO_2 assimilation and H_2O transpiration has been validated in terms of water use efficiency, generally declined when plants subjected to water-deficit stress[18]. Overall growth inhibition, leaf chlorosis (chlorophyll degradation), leaf burn and leaf falling of tropical species in summer and winter seasons are evidently observed[19]. Sensitivity of plant species to water shortage in the dry season (water shortage) has been well established in terms of visual symptoms, i.e., survival percentage[20], relative mortality rate[21], drought index[22] and wilting state[23]. Furthermore, the agroforestry design relating to light requirements and their adaptive abilities to water limited conditions is still lacking. The aim of this study was to assess differences in physiology in responses to varying water availability and light intensity for the establishment of novel agroforestry systems, relating to individual requirements of plant species.

MATERIALS AND METHODS

Plant materials and treatments

Seeds of *Dipterocarpus alatus* and *D. tuberculatus* were collected from the mixed deciduous forest in the northern region of Thailand, and germinated in plastic bags containing mixed soil (electrical conductivity 2.687 dS/m; pH 5.5; organic matter 10%; total nitrogen 0.17%; total phosphorus 0.07%; total potassium 1%). One year-old *Hevea brasiliensis* scion cv. RRIM 600 on wild root stock was cultivated in clay pot culture and *Eucalyptus camaldulensis* plantlets derived from micropropagation[24] were transplanted and grown in a greenhouse under 500–1000 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) with a 10 h per day photoperiod, temperature 28 ± 2 °C, and 80 ± 5% relative humidity (RH). Corms of *Colocasia esculenta* and *C. gigantea* were collected from swamp habitat in the northern region of Thailand. The plants were divided into two groups: (a) well watering (WW) (2 times daily irrigation) and (b) water deficit (WD) condition (water withholding for 7 d) with 5 plants per group. Field capacity (FC, %) was measured and calculated by weighing the plastic bag containing mixed soil at 0, 2, 4, and 7 d after water withholding. Intracellular CO_2 (C_i), net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (E), water use efficiency (WUE) and stomatal density in the leaf tissues were measured. All plants were grown in a greenhouse under 500–1000 μmol m^{-2} s^{-1} PPFD with a 10 h per day photoperiod, 28 ± 2 °C and 80 ± 5% RH in the plastic bag containing mixed soil and incubated in a greenhouse for four months.

Photosynthetic, stomatal function, and WUE

P_n, g_s, E, and WUE of the second fully matured leaf from the shoot tip was measured by a portable photosynthesis system connected to an infra-red gas analyser (Model LI 6400XT, LI-COR Inc., Lincoln, NE, USA). The air-flow rate of sample chamber was 500 μmol CO_2 s^{-1} at 25 °C and the light intensity was 1000 μmol m^{-2} s^{-1} PPFD of 6400-02B red-blue LED light source. Light response curve in each plant species was derived based on auto-measurement at 0, 50, 100, 250, 500, 750, 1000, and 1500 μmol m^{-2} s^{-1} (PPFD or PAR$_i$). WUE was calculated according to a ratio of P_n and E.

Stomatal density assay

Clear nail polish was painted on the abaxial surface of the leaf, until dry, then peeled from the leaf using Scotch Tape (transparent type, Scotch) subsequently mounted peel in a grid (0.0625 mm^2) under a compound 400× light microscope (model Axiostar*plus*, Carl Zeiss NY, USA) connected with a Motic microscope camera (Motic, Hong Kong) and the number of stomata observed under 5 fields of each peel was recorded[25].

Experiment design and statistical analysis

The experiment was arranged in completely randomized design with five replicates ($n = 5$). The mean values obtained in each plant under well watering and water-deficit stress were compared using t-test and analysed with SPSS (version 11.5).

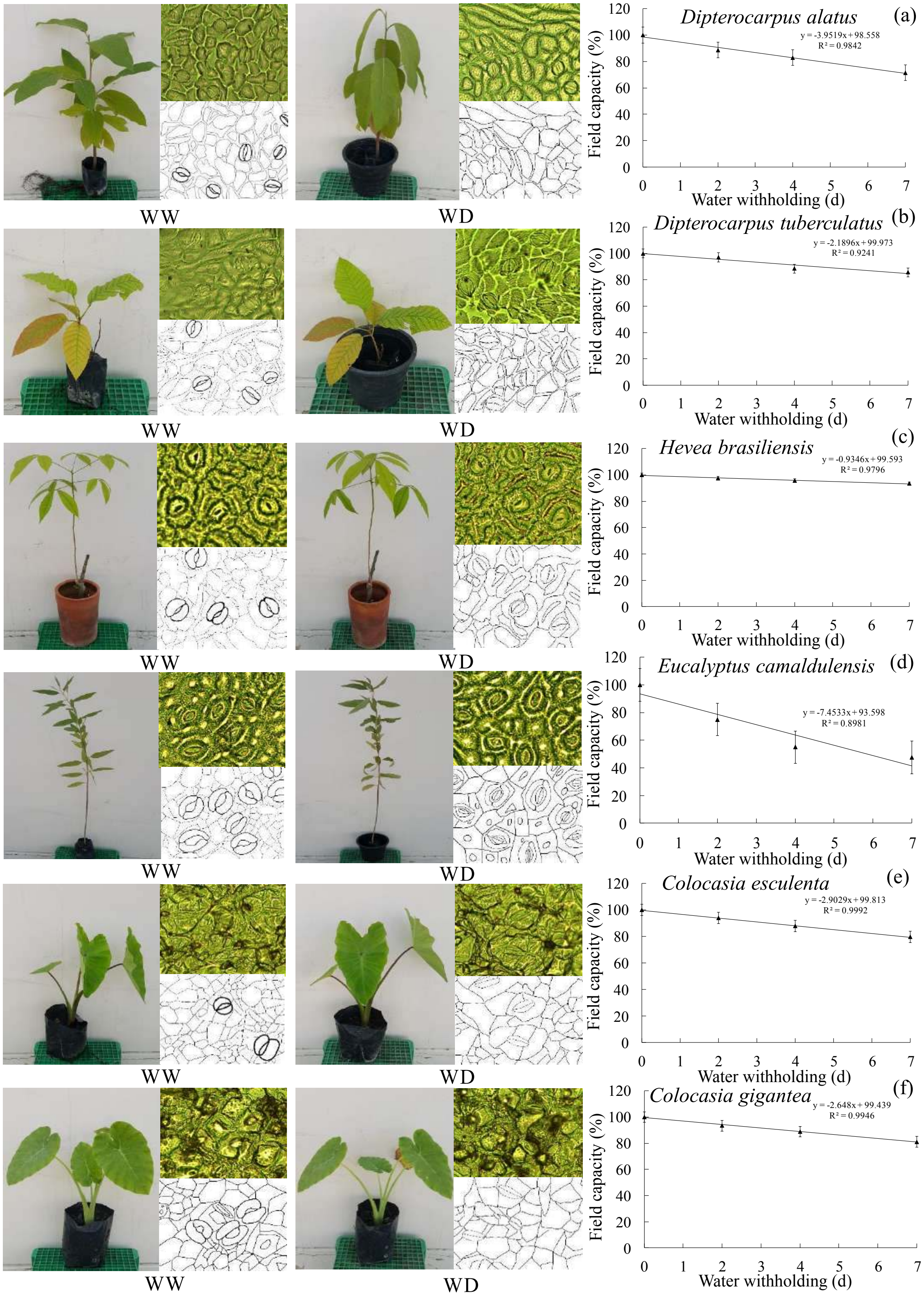

Fig. 1 Morphological characteristics, stomatal density in the plant grown under well watering (WW) and decline field capacity (%) in the soil substrate after water withholding for 7 days.

Table 1 Net photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (E), water use efficiency (WUE), and stomata density in *D. alatus* Roxb. ex G. Don, *D. tuberculatus* Roxb., *H. brasiliensis* Muell. Arg., *E. camaldulensis* Dehnh., *C. esculenta* (L.) Schott, and *C. gigantea* Hook. f. grown under well watering (WW) and water deficit (WD) conditions. Standard errors were expressed as mean ± SE.

Plant species	Water	P_n	g_s	E	WUE	Stomatal density
D. alatus	WW	2.91 ± 0.19^a	0.051 ± 0.002^a	1.48 ± 0.06^a	19.8 ± 1.4^a	6.00 ± 0.84
	WD	0.34 ± 0.03^b	0.016 ± 0.001^b	0.30 ± 0.02^b	11.6 ± 1.0^b	5.80 ± 0.97
		(88%)	(69%)	(80%)	(42%)	
D. tuberculatus	WW	4.88 ± 0.27^a	0.064 ± 0.004^a	1.40 ± 0.08^a	34.7 ± 3.0^a	6.20 ± 0.58
	WD	0.89 ± 0.05^b	0.020 ± 0.003^b	0.57 ± 0.08^b	15.8 ± 1.3^b	5.40 ± 0.68
		(82%)	(69%)	(22%)	(54%)	
H. brasiliensis	WW	2.49 ± 0.10^a	0.057 ± 0.001^a	1.10 ± 0.03^a	22.5 ± 0.4^a	4.60 ± 0.51
	WD	1.69 ± 0.13^b	0.010 ± 0.001^b	0.86 ± 0.02^b	19.7 ± 1.1^b	3.60 ± 0.51
		(32%)	(82%)	(22%)	(12%)	
E. camaldulensis	WW	6.60 ± 0.33^a	0.083 ± 0.005^a	2.72 ± 0.12^a	24.5 ± 1.6^a	6.00 ± 0.63
	WD	0.71 ± 0.04^b	0.007 ± 0.001^b	0.42 ± 0.03^b	17.2 ± 0.6^b	5.80 ± 0.49
		(89%)	(92%)	(85%)	(30%)	
C. esculenta	WW	6.97 ± 0.23^a	0.102 ± 0.002^a	2.25 ± 0.04^a	31.1 ± 1.2^a	2.20 ± 0.37
	WD	3.39 ± 0.05^b	0.038 ± 0.003^b	1.40 ± 0.06^b	24.3 ± 1.0^b	1.60 ± 0.40
		(51%)	(63%)	(38%)	(22%)	
C. gigantea	WW	3.55 ± 0.15^a	0.042 ± 0.004^a	2.25 ± 0.04^a	31.1 ± 1.2^a	2.00 ± 0.32
	WD	1.68 ± 0.12^b	0.014 ± 0.001^b	1.40 ± 0.06^b	24.3 ± 1.0^b	1.40 ± 0.25
		(53%)	(67%)	(38%)	(22%)	

Different letters in each column show significant difference at $p \leqslant 0.01$ by t-test. Parentheses represent reduction percentage of water-deficit stressed plants compare to well watering in each parameter.

RESULTS

Morphological and physiological responses to WD condition

Field capacity (%) of the soil decreased depending on the duration water withholding. After 7 d water withholding period, FC sharply declined in the plastic bag containing *E. camaldulensis* plant (48% FC), with leaf burn symptoms. Furthermore, 71% FC was measured in the soil containing *D. alatus*, with initiation of wilting symptoms. In contrast, FC measured in the soil of *C. gigantea*, *C. esculenta*, *D. tuberculatus* and *H. brasiliensis* were 80%, 85%, 86%, and 93%, respectively, without any morphological changes after 7 d water withholding (Fig. 1). There was no significant difference in stomatal density among treatments (Table 1), whereas stomatal closure in all plant species under water deficit condition was observed (Fig. 1).

In the present study, P_n, g_s, E, and WUE were sensitive to a degree of FC reduction in the soil (Table 1). In *E. camaldulensis*, P_n, g_s, E, and WUE in plants under 48% FC were dropped by 89%, 92%, 85%, and 30%, respectively, when compared with well watering. Likewise, these parameters in *D. alatus* were declined by 88%, 69%, 80%, and 42%, respectively, when subjected to 71% FC. P_n, g_s, and WUE in *D. tuberculatus* under 86% FC were diminished by 82%, 69%, and 54%, respectively. Interestingly, these parameters in *Colocasia* species were slightly decreased when exposed to 85% FC (Table 1). In *H. brasiliensis*, the FC maintained at 93% resulted in high P_n, E, and WUE.

Light response curves under WD condition

In emergent layers of *Dipterocarpus* spp., intracellular CO_2 (μmol CO_2 mol $^{-1}$) was declined, causing an increased input of photosynthetically active radiations (PAR_i). C_i in well-watered plants of *D. alatus* was higher than that in water deficit condition, while it was unchanged in *D. tuberculatus* (Fig. 2a,b). CO_2 assimilation rate or P_n in both *D. alatus* and *D. tuberculatus* was increased along with the degree of light intensities (Fig. 2c,d), especially in well-watered plants. *D. tuberculatus* was sensitive to light intensity (Fig. 2d). In water deficit condition, it was slightly increased when compared with well watering (Fig. 2c,d). Furthermore, a positive relation between g_s and E in *D. alatus* ($R^2 = 0.987$) and *D. tuberculatus* ($R^2 = 0.921$) was

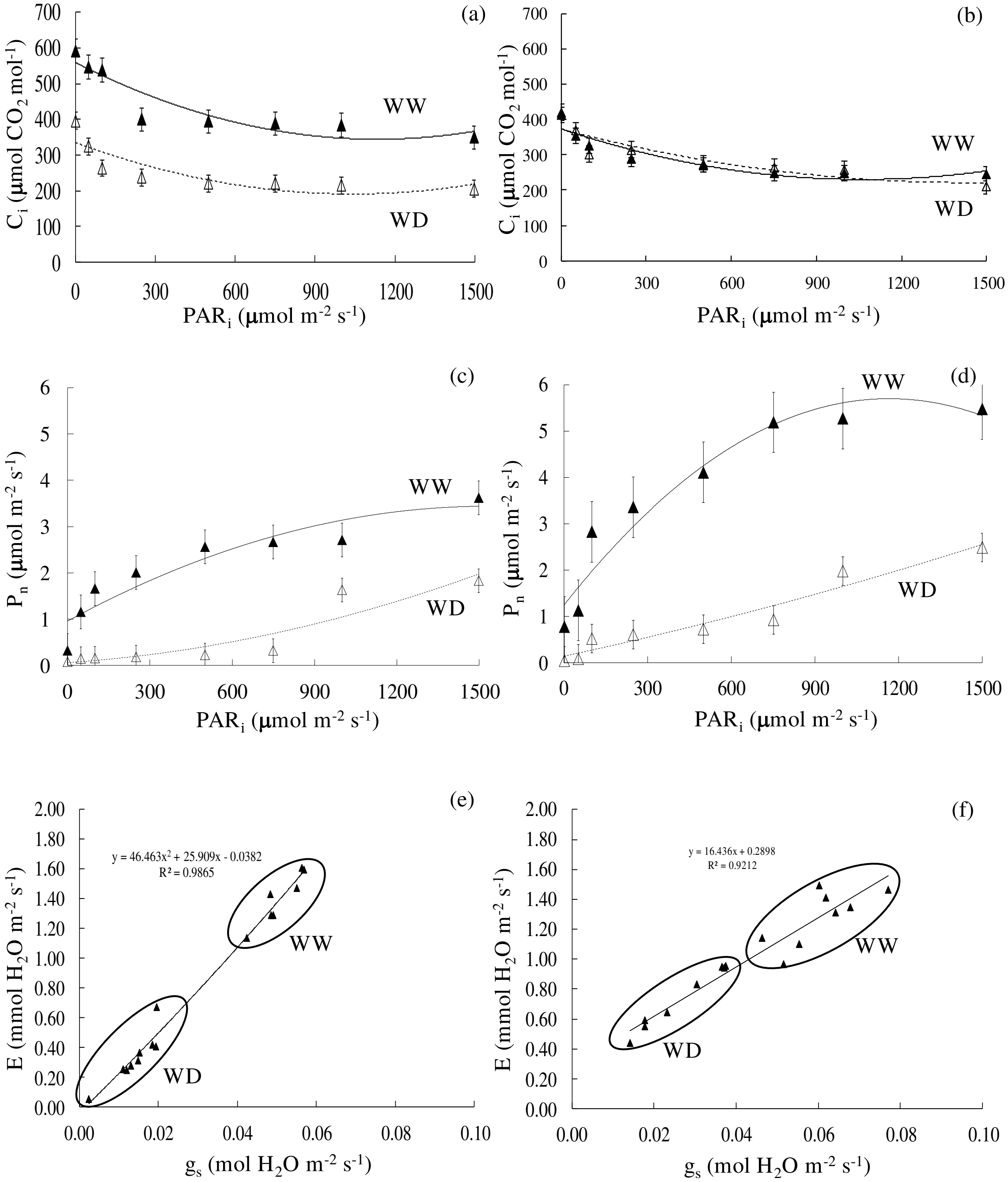

Fig. 2 Response of (a,b) intracellular CO_2 (C_i) and (c,d) net photosynthetic rate (P_n) to light intensity flux (PAR_i) and (e,f) relationship between stomatal conductance (g_s) and transpiration rate (E) in (a,c,e) *D. alatus* Roxb. ex G. Don and (b,d,f) *D. tuberculatus* Roxb. grown under well watering (WW) and water deficit (WD) conditions.

demonstrated (Fig. 2e,f).

In canopy layers of mono-plantation, C_i in *H. brasiliensis* and *E. camaldulensis* trees under water deficit condition was decreased according to increased light intensity, whereas it was unchanged under well watering condition (Fig. 3a,b). Interestingly, C_i in *E. camaldulensis* under water deficit was better than well watering (Fig. 3b) whereas it was lower in *H. brasiliensis* (Fig. 3a). *E. camaldulensis* was identified as light sensitive based on the increase in P_n in response to high light intensity (Fig. 3d). In water-deficit stress, P_n in *H. brasiliensis*

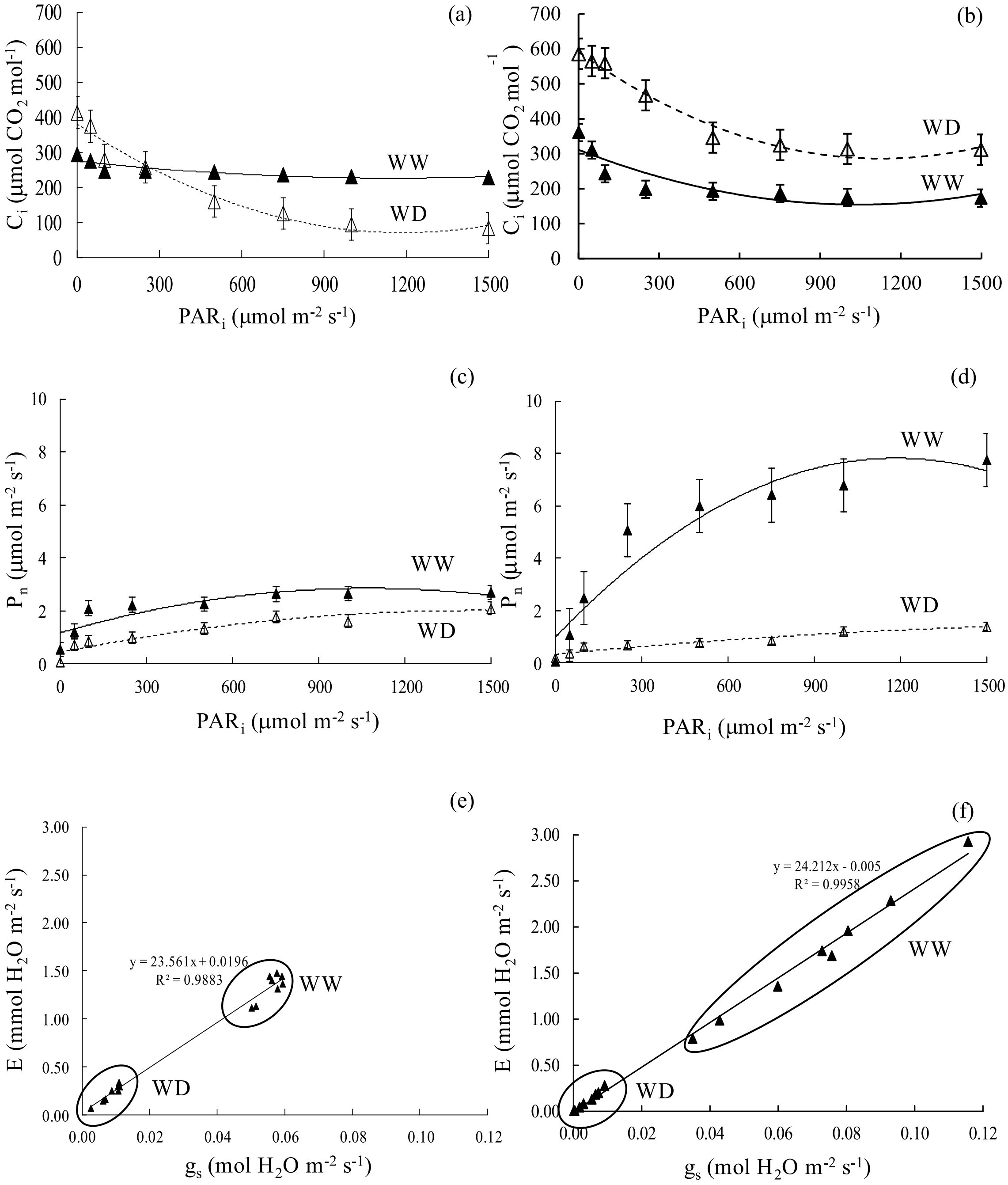

Fig. 3 Same as Fig. 2, for (a,c,e) *H. brasiliensis* Muell. Arg. and (b,d,f) *E. camaldulensis* Dehnh.

was maintained, but P_n of *E. camaldulensis* plant was very low in each light flux when compared with well-watered plants (Fig. 2c,d). Progressive relationships between g_s and E in *H. brasiliensis* ($R^2 = 0.988$) and *E. camaldulensis* ($R^2 = 0.996$) were demonstrated (Fig. 3e,f).

In ground cover layer, C_i in *Colocasia* species showed a similar trend of decrease in response to high light intensity in both well watering and water limited conditions (Fig. 4a,b). The P_n for *C. esculenta* under WW and WD was unchanged at high light intensity. Similarly, P_n was increased with an increase in PAR$_i$ (Fig. 4c,d). A positive relation between g_s and E in *C. esculenta* ($R^2 = 0.807$) and *C. gigantea* ($R^2 = 0.971$) was demonstrated (Fig. 4e,f).

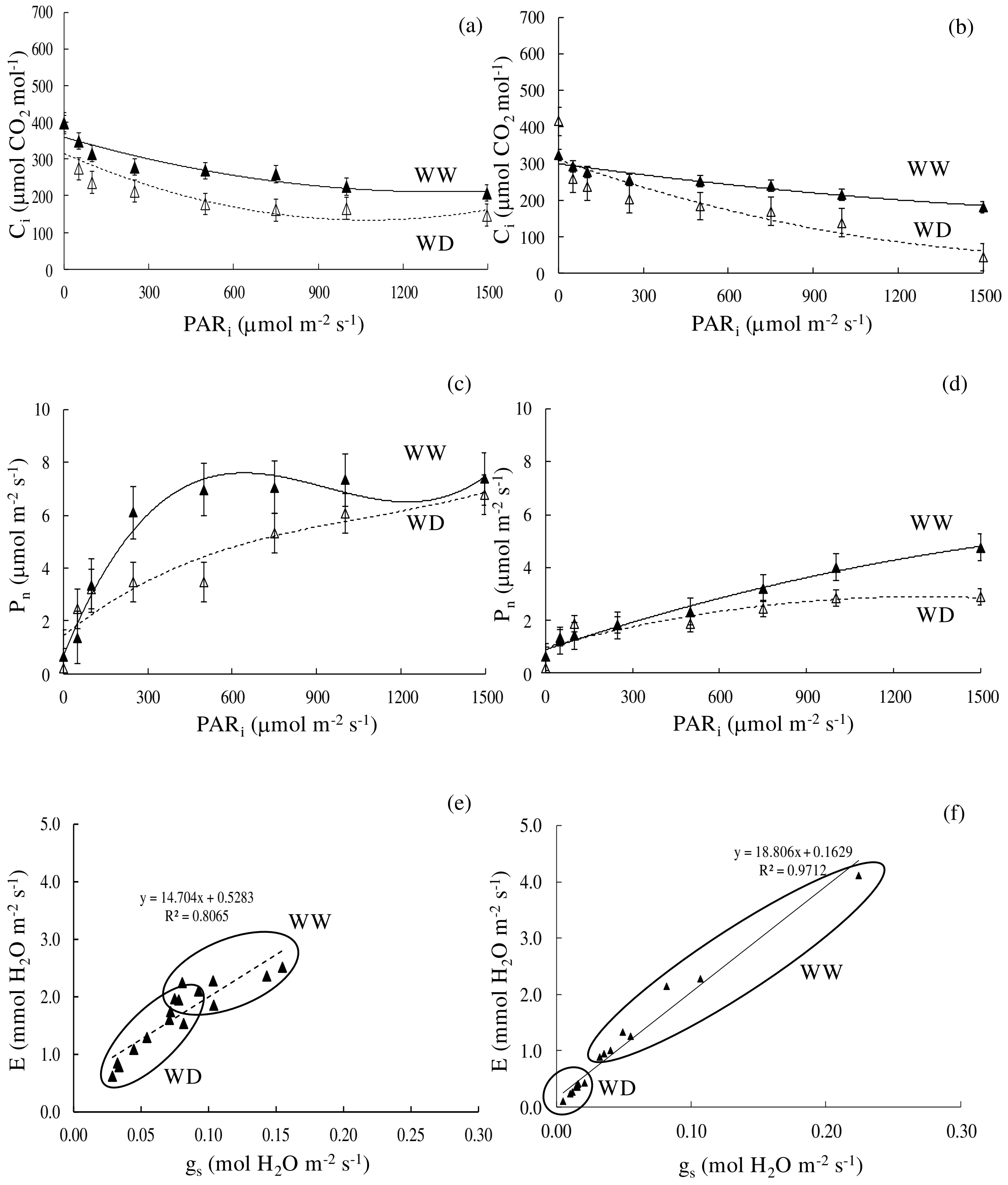

Fig. 4 Same as Fig. 2, for (a,c,e) *C. esculenta* (L.) Schott and (b,d,f) *C. gigantea* Hook. f.

DISCUSSION

In the present study, the plant injuries such as leaf chlorosis, leaf burn, plant wilting, and plant death depend on plant species and the water availability in the soil. Previously, the wilting state and mortality of plants under dry season in nine forest species have been categorized into two clusters: cluster I (low survival rate with high wilting score or drought susceptible group) including *Beilschmiedia pendula*, *Calophyllum longifolium*, *Sorocea affinis* and *Tabebuia rosea*, and cluster II (high survival rate with low wilting score or drought sensitive group) including *Garcinia intermedia*, *Hybanthus prunifolius*, *Ouratea lucens*, *Pseudobombax septenatum* and *Psychotria horizontalis*[22]. In the present study, stomatal density among treatments was unaffected, whereas the stomatal conductance in all plant species under water deficit condition was declined. In a study using 29 genotypes of poplar, total stomata density in plants grown under well-watered (757 stomata mm^{-2}) and water deficit conditions (769 stomata mm^{-2}) was unchanged, while stomatal conductance or stomatal closure in plants under water deficit declined by 28% when compared with well-watered conditions[26]. In contrast, the stomatal density in olive changed under longer durations of water deficit[16, 18].

In general, the stomatal closure relating to g_s and E reduction was evidently observed when plants were subjected to water deficit, resulting in limited CO_2 assimilation. In the present study, P_n, g_s, E, and WUE reduction in several plant species under water shortage situation was described. Similar reductions in P_n (74% of control), g_s (75% of control), and E (92%) were observed in plants in response to water-deficit stress (25% FC) in *Populus przewalskii*[27]. In addition, rainy and dry seasons introduce a large gap of water availability in the soil, leading to retardation of photosynthetic abilities. For example, photosynthetic capacity (A_{max}) in *D. retusus*, *Hopea hainanensis*, *Parashorea chinensis*, and *Vatica xishuangbannaensis* under dry season was decreased by 52%, 52%, 58%, and 63%, respectively, when compared with the rainy season[28]. A_{max} and g_s in *Miconia ciliata* are very low in the dry season, subsequently lifting up by irrigation and wet season[29]. In addition, P_n and g_s in Bornean heath forest including *Cotylelobium burckii*, *D. borneensis*, *H. pentanervia*, *Shorea multiflora*, *Fordia splendidissima*, *Tristaniopsis obovata*, and *Cleistanthus baramicus* in the dry season (December–April) are decreased[30]. The decline in these parameters depends on plant species[31] and the degree of drought stress[32].

A decrease in C_i in response to PAR_i in each plant genotype was established. A rate of C_i reduction depending on the plant species and the degree of water deficit conditions was observed. The decrease in C_i of well-watered plants of *Jatropha curcas* cultivars in Indonesia and Cape Verde islands was confirmed in relation to increased PPFD[31]. In general, C_i of well-watered plants was maintained at a higher level than in water stressed plants[17, 33]. In the dry season, C_i of controlled plants of *M. ciliata* was lower than that of irrigated plants and it increased in the rainy season[29]. Interestingly, the C_i in water stressed *E. camaldulensis* was accumulated in the higher concentrations than that of well-watered plants. Leaf burn was evidently observed in *E. camaldulensis* under water deficit, leading to high levels of intracellular CO_2. Similar results have been reported in *Vitis vinifera* cultivars Khoshnave, Askan, and Bidane-Sefid that showed an increase in C_i when plants were subjected to the enhanced degree of water-deficit stresses[32]. In addition, C_i in *D. tuberculatus* was retained in both WW and WD conditions. In general, the C_i in *Podocarpus lawrencei* plants grown under drought condition fluctuates relating to CO_2 assimilation rate ($R^2 = 0.935$) and it fits to the linear curve in both watered and unwatered plants[34].

CO_2 assimilation rate or P_n in the leaf tissues of each plant species was increased in relation to the density of light flux. Furthermore, P_n in the plants grown under water deficit conditions was slightly increased and demonstrated a big gap between well-watered and water stressed plants, especially in *D. alatus*, *D. tuberculatus* and *E. camaldulensis*, which was evidently demonstrated by the visual symptoms such as wilting, leaf chlorosis and leaf burn, respectively. In addition, the P_n of four dipterocarp species, i.e., *D. retusus*, *H. hainanensis*, *P. chinensis*, and *V. xishuangbannaensis* under dry season was lower than that under rainy season[28]. Based on P_n reduction with light response curve in *P. cathayana* when subjected to 30% FC, the reduction rate was more in female plants than in male plants[35], indicating higher sensitivity of female plants towards the drought conditions. In addition, P_n in water-deficit stress of *C. esculenta* was sustained nearby in unstressed plants. It possible that an enriched epicuticular wax in the abaxial leaves may play a key role as water loss prevention when subjected to water deficit[36]. Likewise, there are some other factors in the light responses when plants were exposed to water deficit conditions, i.e., leaf position (exposed and shaded leaves)[37, 38], and a strength of water-deficit stresses in *Eragrostis curvula*[39], *Quercus ilex*[40], *H. brasiliensis*[41], *Lycium nodosum*[42], and *Tamarix chinensis*[43]. A reduction in g_s and E in each plant grown under water deficit condition was evidently established and subsequently a positive relation was observed[44, 45]. In addition, a positive relation between g_s and P_n in leaves of *L. nodosum* ($R^2 = 0.87$)[42], *Vitis vinifera* ($R^2 = 0.83$)[32] and *Symplocos racemosa* ($R^2 = 0.80$)[46] was demonstrated.

In conclusion, the toxic symptoms, i.e., wilting (in *D. alatus*), leaf chlorosis (in *D. tuberculatus*), and leaf burn (in *E. camaldulensis*) were evidently observed when the water availability in the soil was declined, leading to stomatal closure to prevent wa-

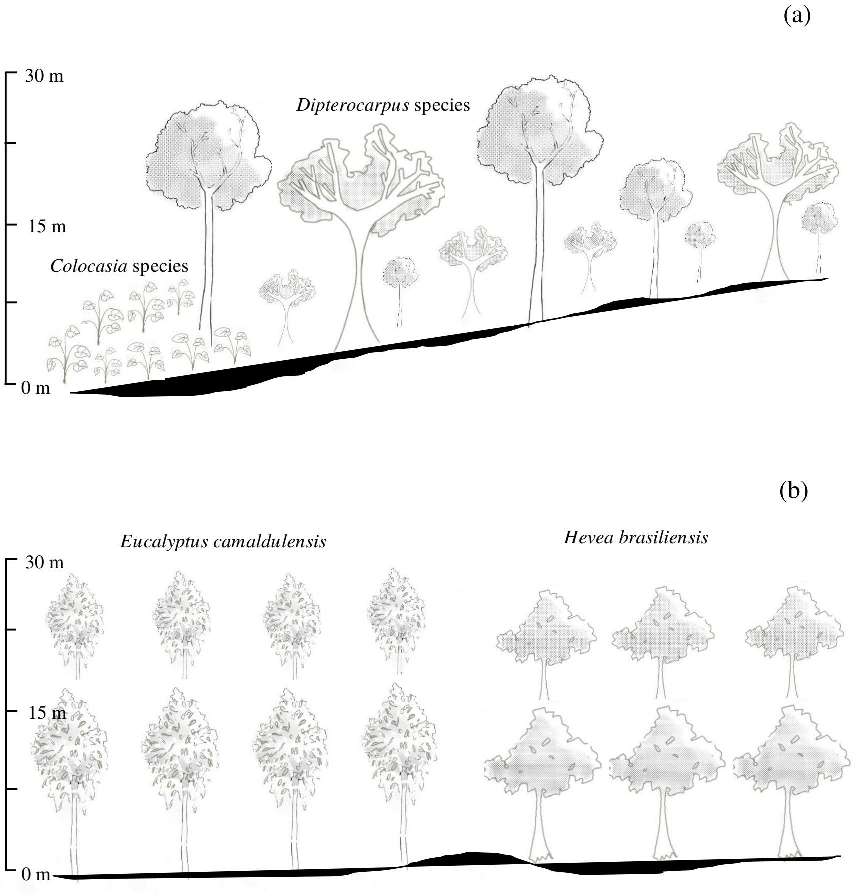

Fig. 5 (a) A scheme of mixed deciduous forest with *C. esculenta* (L.) Schott and *C. gigantea* Hook. f. grown under high humidity with shading light environments. (b) A scheme of monoculture farmed forest species including *E. camaldulensis* and *H. brasiliensis*.

ter loss and consequently reduced assimilation rate. Based on the photosynthetic response, eucalyptus demands more water supply and high light intensity when compared with rubber tree, which is generally grown as mono-plantation. In addition, the light response curve was a key indicator of water deficit conditions in case of emergent layer, canopy layer, and ground cover layer, and it should be managed while planning the mixed deciduous plantations and mono-plantation strategies as demonstrated in the models (Fig. 5).

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