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Original Article

Physiological traits contributing to carbon storage variation in Monastery bamboo and Pai Liang in northeastern Thailand

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Abstract

This study aims at comparing the carbon storage ability of Monastery bamboo (*Thyrsostachys siamensis* Gamble) and Pai Liang (*Dendrocalamus membranaceus* × *Thyrsostachys siamensis*) in terms of the different physiological responses to the microclimate. The stomatal conductance, leaf-to-air vapor pressure deficit (LAVPD), chlorophyll content, and water use efficiency (WUE) were measured. Pai Liang had a greater dry biomass per culm than Monastery bamboo, resulting in more carbon storage. Monastery bamboo kept opening its stomata even when LAVPD increased, resulting in the loss of more water and a lower WUE leading to a lower rate of growth and carbon storage. Pai Liang contained higher amount of carbon and nitrogen in the leaf tissue, indicating a better WUE. With regards to the climate change, Pai Liang is recommended owing to a greater carbon fixation and more rapid growth rate compared to the Monastery bamboo.

Keywords: Monastery bamboo, Pai Liang, leaf-to-air vapor pressure deficit, water use efficiency, carbon storage

1. Introduction

Bamboo is a primitive plant which belongs to the same family as grasses (Poaceae) with a hollow stem called culm and caryopsis seeds (Lucas, 2013). Bamboo has an economic viability in countries such as India, China, Japan (Lobovikov *et al.*, 2005), and Thailand due to its rapid growth, high production, and fast maturity. Due to climate change concerns, carbon storage has been an issue addressed in the world during the last decade (Bunker *et al.*, 2005; Fang *et al.*, 2001; Zhuang *et al.*, 2015). Carbon storage and its long term sequestration have been proposed as means to reduce the rate of accumulation of greenhouse gases such as carbon dioxide. Forests are considered to be the main carbon sink in an ecological system (Secretariat of the Convention on Biological Diversity, 2011) due to its ability to store carbon. According to the IPCC, national greenhouse gas inventories have been divided into five sectors and forest sector is the only one that removes the greenhouse gases from the atmosphere while the rest emits greenhouse gases (*United Nations Framework Convention on Climate Change* [UNFCCC], 2015).

Carbon storage is directly measured from dry biomass. Bamboo has a great carbon storage potential due to its fast-growing characteristic at approximately 0.5 m per week (Scurlock *et al.*, 2000). Song *et al.* (2011) reported that the annual carbon fixation in a bamboo forest was about 1.3-1.4 times higher than in a tropical mountain rain forest and

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Chinese fir forest. Due to a higher rate of carbon storage, bamboo should be considered as one of the most important species for addressing climate change issues. Bamboo forests in Thailand cover approximately 261,000 ha (Lobovikov *et al.*, 2005) or 0.51% of the total land area (1.60% of total forest area), which also adds up as a carbon sink for the ecosystem. Therefore, increasing bamboo areas can potentially help the climate change situation.

Some physiological characteristics, like stomatal conductance directly contribute to bamboo's fast growth (Haworth *et al.*, 2015). Gas exchange process at stomata is a tradeoff between the diffusion of carbon dioxide into the leaf for photosynthesis and water vapor diffusion out of the leaf by transpiration (Lambers *et al.*, 1998). Ratio of carbon assimilation to transpiration is well known as the water use efficiency (WUE) (Farquhar and Richards, 1984). Plants with higher WUE tend to have greater growth rate than plants with lower WUE (Marshall *et al.*, 2007). Stomatal aperture is response to microenvironments such as water in the soil, air dryness, wind velocity, light intensity, temperature, leaf-to-air vapor pressure deficit (LAVPD), and so on (Taiz & Zeiger, 2006). LAVPD being the difference in vapor pressure between leaf and ambient air is generally believed to drive the transpiration process and directly affects the gas exchange process (Farquhar, 1978). Therefore, variations in physiological characteristics in different bamboo species will lead to differences in growth and ultimately their carbon storage ability.

Monastery bamboo and Pai Liang are common in Thailand and have been used as food and in construction materials. Both bamboo species are closely related but only Monastery bamboo can be found in the natural forest while Pai Liang occurs only in plantations. The current studies of bamboo species have mainly emphasized on their growth with regards to the economic aspect, such as how many culms per year can be harvested while, only a few studies have focused on essential factors contributing to their growth. This paper aims at (1) studying the physiological characteristics that affect the growth of these two commonly used bamboo species found in Thailand and to compare their growth rate, (2) estimating their dry biomass to compare the ability of carbon storage between the two species, and (3) suggesting a species that is viable both from commercial and environmental stand point.

2. Materials and Methods

2.1 Study site

The study was done in the Chaloem Phra Kiat King Rama 9th Forest Species Central Park, Wang Nam Khiao district, Nakhon Ratchasima province, Northeastern Thailand (14°30'10.9" N 101°56'59.8" E) with a total area of 7,900 square meters and approximately 300-700 m above sea level (Figure 1). Based on a 44-year period climate data (1970-2014;

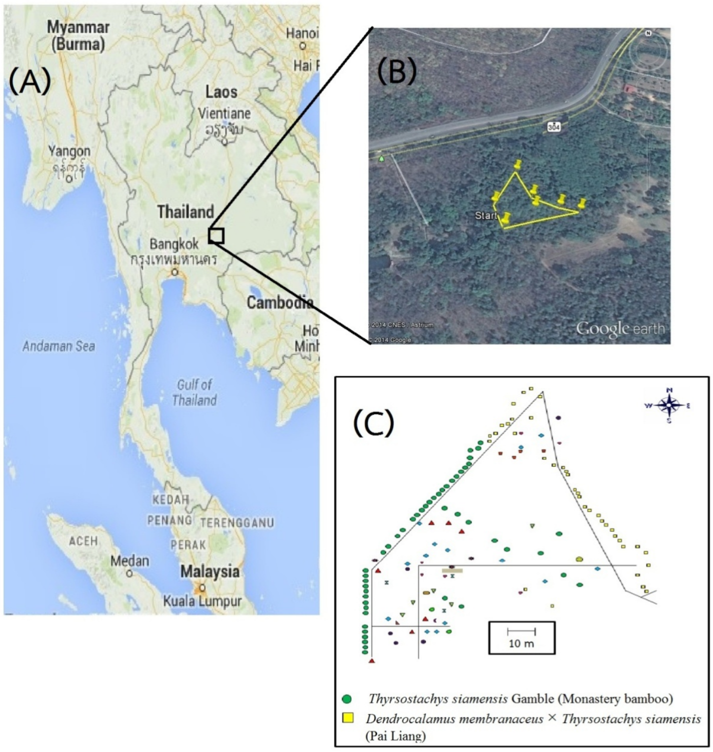

Figure 1. Study area at Chaloem Phra Kiat King Rama 9th Forest Species Central Park, Wang Nam Khiao district, Nakhon Ratchasima province, Northeastern Thailand (14°30'10.9" N 101°56'59.8" E) with a total area of 7,900 square meters (A,B). Bamboo species distribution of *Thyrsostachys siamensis* Gamble (Monastery bamboo; green circle), *Dendrocalamus membranaceus* × *Thyrsostachys siamensis* (Pai Liang; yellow square) and other species in the study area (C).

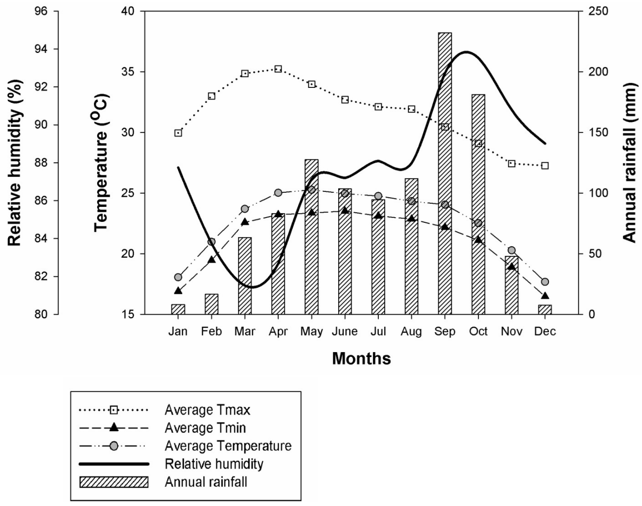

Figure 2. Monthly weather conditions in the study area during the 44-year period (1970 -2014) with the average maximum temperature (open squared with dotted line), average minimum temperature (closed triangle with short line), average temperature (closed circle with shot-dotted line), relative humidity (solid line) and annual rainfall during each month (bars).

Figure 2), the summer season occurs from March to May with an average temperature between 32-35°C and relative humidity (RH) between 82-87%. Rainy season occurs during June to October with a lower temperature and higher relative humidity (RH). Soil texture is sandy loam with slight acidity (pH 4.9-5.7), and low in nutrition.

2.2 Plant materials

Both Thai and Pai Liang were planted within the same year and allowed to naturally grow and reproduce for more than ten years. Therefore, the study areas resemble a natural forest. Every single culm with a circumference larger than 4 cm, at a height of 1.30 m above the soil surface was measured and the size class distribution of culm circumference analyzed (Figure 3).

2.3 Measurements

Measurements were conducted from August 2013 to July 2014.

2.3.1 Dry biomass and carbon storage

Allometric equation, widely used for non-destructive methods to estimate the dry biomass (Chaiyo *et al.*, 2012; Yen *et al.*, 2010), was used in this study. An allometric equation was created based on an increasing circumference from the lowest to the highest range of each species (4.0-20.0 in Monastery bamboo and 5.5-21.0 cm in Pai Liang) to represent the whole stand. One culm at incremental circumferences of 0.5 cm (a total of 31 culms for each species) was harvested, with the culm and leaves analyzed separately. Each culm was cut at every node and measured for culm thickness, internode length, and culm weight. Ten leaves from each culm were chosen to measure the length and width, as described in Table 1. Culms and leaves were then oven-dried at a temperature of 110°C for 48 hours and the dry weight determined to be used as dry biomass. The culm and leaf moisture content was calculated using the equation,

Moisture content =

$$\text{(wet weight} - \text{dry weight)/ dry weight} \times 100 \quad (1)$$

The relationship between the total dry biomass and culm size (or the diameter at breast height (DBH) = circumference at 1.30 m height/π), total height, and the internode length at 1.30 m height can be expressed by the equation (Trombulak, 1991):

$$Y = a\,X^b \quad \text{or} \quad \text{Log } Y = \text{Log } a + b \text{ Log } X. \quad (2)$$

In the above equation, Y is the dependent variable or dry biomass (g), X is one of the various independent variables, which include the DBH, total height, and the internode length, while a and b are the fitted coefficients. As indicated in Table 2 and 3, from the different combinations, the equation

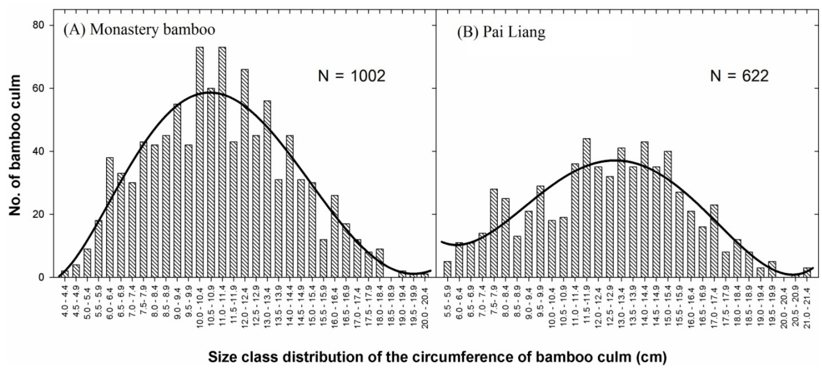

Figure 3. Culm size frequency in (A) Monastery bamboo and (B) Pai Liang at Wang Nam Khiao district, Nakhon Ratchasima province, Thailand. The culm circumference varied between 4.0-20.0 cm (5.5-21.2 cm) in a total number of culms of 1,002 (662) for Monastery bamboo (Pai Liang), respectively.

Table 1. Morphological characteristics in Monastery bamboo and Pai Liang at Wang Nam Khiao district, Nakhon Ratchasima province, Thailand. The average ± Standard Error (SE) is presented, with N being the sample size or the total number of culms in the area of study.

Characteristics	Monastery bamboo	Pai Liang	*P-Value*
Average culm thickness ± SE (cm)	$0.61±0.03^{b}$*	$0.83±0.04^{a}$	*<0.0001*
[range] (N= 1000)	[0.22-0.89]	[0.53-1.11]	
Average internode length ± SE (cm)	$25.05±0.83^{b}$	$29.38±0.65^{a}$	*<0.0001*
[range] (N= 1000)	[16.10-32.83]	[21.11-36.25]	
Average leaf length ± SE (cm)	$7.89±0.23^{b}$	$9.26±0.23^{a}$	*<0.0001*
[range] (N= 240)	[3.6-13.0]	[1.5-14.0]	
Average leaf width ± SE (cm)	$0.55±0.02^{b}$	$0.82±0.05^{a}$	*<0.0001*
[range] (N= 240)	[0.4-1.0]	[0.7-1.6]	
Moisture content in culms ± SE (%)	$76.64±4.89^{NS}$	$87.21±3.35^{NS}$	*0.094*
Moisture content in leaf ± SE (%)	$71.73±3.06^{NS}$	$64.28±2.31^{NS}$	*0.114*

* Means with the different letters in the row were statistically different at significance level of P-value < 0.05. NS means no statistical difference between the means of two bamboo species.

Table 2. Possible allometric equations for culm and leaf dry biomass (kg) estimation in Monastery bamboo. The chosen equation to estimate the carbon storage is indicated in bold based on a P-value <0.05, high R^2 and a low standard error (SE). The form of the allometric equation was $Y= aX^b$ or Log Y = b Log X + Log a. Where Y = dry biomass in kg and X = independent variable(s).

Independent variables (X)	Equation	a	b	SE	R^2	P-Value
			Culm			
1) DBH (cm)	LogY = 2.143 X + 2.180	151.356	2.143	0.160	0.857	< 0.001
2) DBH^2 (cm^2)	**LogY = 1.072 X + 2.180**	**151.356**	**1.072**	**0.080**	**0.857**	**< 0.001**
3) DBH × Total height (cm ×m)	LogY = 1.199 X + 0.329	2.133	1.199	0.084	0.871	< 0.001
4) DBH × Length at 1.30 m (cm ×m)	LogY = 1.506 X + 0.558	3.614	1.506	0.154	0.759	< 0.001
5) DBH^2 × Total height (cm^2 ×m)	LogY = 0.772 X + 0.982	9.594	0.722	0.054	0.870	< 0.001
6) DBH^2 × Length at 1.30 m (cm^2 ×m)	LogY = 0.908 X + 1.171	14.825	0.908	0.077	0.822	< 0.001
			Leaf			
1) DBH (cm)	LogY = 1.435 X + 1.784	60.813	1.435	0.584	0.180	0.022
2) DBH^2 (cm^2)	**LogY = 0.717 X + 1.784**	**60.813**	**0.717**	**0.292**	**0.180**	**0.022**
3) DBH × Total height (cm ×m)	LogY = 0.771 X + 0.623	4.198	0.771	0.344	0.148	0.036
4) DBH × Length at 1.30 m (cm ×m)	LogY = 0.805 X + 1.093	12.388	0.805	0.457	0.084	0.092
5) DBH^2 × Total height (cm^2 ×m)	LogY = 0.505 X + 1.015	10.35	0.505	0.217	0.161	0.030
6) DBH^2 × Length at 1.30 m (cm^2 ×m)	LogY = 0.558 X + 1.233	117.100	0.558	0.264	0.132	0.046

DBH represents the diameter of the culm (in cm). a and b are the fitted coefficients of allometric equation $Y= aX^b$. SE is standard error of the equation. R^2 is the coefficient of determination ranging from 0-1. P-value is the test of the coefficient at the level of P-value < 0.05 which means the model is meaningful because the changes in the predictor's value (X) are related to changes in the response variable (Y).

used to calculate the dry biomass and associated carbon storage was chosen based on the simplicity of the independent parameter in equation, low standard error (SE), high coefficient of determination (R^2), and the slope of regression that had a P-value less than 0.05.

After a best fit allometric equation was selected, carbon storage was calculated based on the guidelines listed in the national greenhouse gas inventories (IPCC, 2006), which suggests that the carbon stored in plants could be determined by multiplying the dry biomass with a convertor number (0.47). After the carbon storage of all culms were calculated and summarized, the carbon storage per culm in each species was estimated by dividing total carbon storage with the total number of culms (1,002 for Monastery bamboo and 622 for Pai Liang), as presented in Table 4.

Table 3. Possible allometric equations for culm and leaf dry biomass (kg) estimation in Pai Liang. As in Table 2, the equations highlighted in bold were used to calculate the carbon storage in the culm and the leaf. The same form of allometric equation and least significance difference test was used as for the Monastery bamboo.

Independent variables (X)	Equation	a	b	SE	R^2	P-Value
Culm						
1) DBH (cm)	LogY = 2.471 X + 2.056	113.762	2.471	0.101	0.952	< 0.001
2) DBH^2 (cm^2)	**LogY = 1.235 X + 2.056**	**113.762**	**1.235**	**0.050**	**0.952**	**< 0.001**
3) DBH × Total height (cm ×m)	LogY = 1.405 X – 0.174	0.670	1.405	0.064	0.940	< 0.001
4) DBH × Length at 1.30 m (cm ×m)	LogY = 1.774 X – 0.026	0.940	1.774	0.208	0.705	< 0.001
5) DBH^2 × Total height (cm^2 ×m)	LogY = 0.907 X + 0.599	3.972	0.907	0.035	0.956	< 0.001
6) DBH^2 × Length at 1.30 m (cm^2 ×m)	LogY = 1.114 X + 0.629	4.256	1.114	0.077	0.875	< 0.001
Leaf						
1) DBH (cm)	LogY = 2.192 X + 1.752	56.493	2.192	0.208	0.786	< 0.001
2) DBH^2 (cm^2)	**LogY = 1.096 X + 1.752**	**56.493**	**1.096**	**0.104**	**0.786**	**< 0.001**
3) DBH × Total height (cm ×m)	LogY = 1.256 X – 0.250	0.562	1.256	0.118	0.788	< 0.001
4) DBH × Length at 1.30 m (cm ×m)	LogY = 1.620 X – 0.189	0.647	1.620	0.230	0.618	< 0.001
5) DBH^2 × Total height (cm^2 ×m)	LogY = 0.808 X + 0.448	2.805	0.808	0.074	0.797	< 0.001
6) DBH^2 × Length at 1.30 m (cm^2 ×m)	LogY = 1.003 X + 0.488	2.805	1.003	0.107	0.745	< 0.001

DBH represents the diameter of the culm (in cm). a and b are the fitted coefficients of allometric equation $Y= aX^b$. SE is standard error of the equation. R^2 is the coefficient of determination ranging from 0–1. P-value is the test of the coefficient at the level of P-value < 0.05 which means the model is meaningful because the changes in the predictor's value (X) are related to changes in the response variable (Y).

Table 4. Estimation of dry biomass using the allometric equation chosen from Tables 2 and 3 (in bold) along with the total carbon storage and carbon storage in each culm of Monastery bamboo and Pai Laing. As indicated by the last column, the Pai Liang stored almost twice the amount of carbon when compared with the Monastery bamboo.

Species	Total dry biomass ($kg\ m^{-2}$)		Total carbon storage ($kg\ m^{-2}$)		Carbon storage in each culm ($kg\ culm^{-1}$)
	Culm	Leaf	Culm	Leaf	
Monastery bamboo (N=1002)	0.310	0.048	0.146	0.022	1.328
Pai Liang (N=622)	0.329	0.107	0.155	0.050	2.607

2.3.2 Stomatal conductance response to microclimate

Stomatal conductance (g_s) was measured in March-April (summer season) and August–September (rainy season), when the vapor pressure in the air was the lowest and highest, respectively. Measurements were conducted every hour from 8:00 am - 4:00 pm, three times during each season using a porometer (Model SC-1 Decagon, Decagon Device Inc., Pullman, WA, USA). Ten mature leaves, (located at the same height of 1.5 m from random bamboo stems of each species) which were under direct sunlight, were measured for their stomatal conductance, by placing the leaf with its lower side facing the chamber. Simultaneously, the temperature of the same leaves (used for g_s measurement) was measured using an infrared thermometer (Model LT760GX Thermometer, Lega Technologies, Co., Ltd., Japan) to calculate the leaf-to-air vapor pressure deficit (LAVPD).

Microclimate data was also collected at the same time as the g_s and leaf temperature measurements. Air temperature was measured using an automated data logger (HOBO Pendant Light intensity and Temperature, Onset Computer Corporation, Bourne, MA, USA). LAVPD was calculated based on the air and leaf temperature as, LAVPD = e_{leaf} - e_{air}, where e_{leaf} is the vapor pressure in the leaf and e_{air} is the vapor pressure in the ambient air. Vapor pressure was calculated using the expression (Murray, 1967):

$$\text{Vapor pressure } (e) = 0.6108 \exp((17.37T/(T+237.3)) \quad (3)$$

where T is the temperature (in deg. Celsius) and e is in unit of kilopascal (kPa).

2.3.3 Chlorophyll content

The chlorophyll content was measured by a non-destructive method using SPAD (Model SPAD-502, Konica Minolta, Inc., Osaka, Japan). During the rainy season (July-August), 275 mature leaves of each species were randomly measured for their chlorophyll content. Each leaf was selected from the same height (1.5 m) and exposed to direct sunlight. Ten measurements were done in order to capture the leaf-level variability in the chlorophyll content.

2.3.4 Water use efficiency

Water use efficiency (WUE) was estimated by the isotopic technique, in which carbon isotope (C^{13}) has been reported to be directly related to WUE (Farquhar and Richards, 1984). WUE is expressed as the ratio of the rate of carbon assimilation (*A*) to transpiration (*E*) in many species and is widely used to indicate the ability of a plant to assimilate carbon through photosynthesis while losing water via its stomata (Flanagan & Farquhar, 2014; Soule & Knapp, 2015). Due to both the carbon isotopic composition and WUE being controlled by the ratio of carbon concentration in the intercellular air space (C_i) and in the ambient air (C_a), the isotopic composition $d^{13}C_{leaf}$ can be expressed as follows (Marshall *et al.*, 2007):

$$\delta^{13}C_{leaf}(‰) = \delta^{13}C_{atm} - a - (b - a)\, C_i/C\text{-}_a \tag{4}$$

where $\delta^{13}C_{atm}$ is –8.1‰, a is the diffusion fractionation (4.4‰), b is the CO_2 fixation fractionation (27‰), and C_i/C_a is the ratio of carbon concentration between intercellular air space and ambient air, respectively. $\delta^{13}C_{leaf}$ is typically reported as a negative fraction of thousand (‰) and a lesser negative value indicates a higher WUE.

WUE and chlorophyll content were measured during the month of September (rainy season), to investigate the WUE at a time when water was not limited. Twenty mature and sunlit leaves of each species, from the same height (1.5 m) were collected, cleaned with deionized water, and dried completely. They were oven-dried at 70°C for 48 hours and samples ground to obtain a powder. The carbon isotopic composition ($\delta^{13}C_{leaf}$) was measured by a mass spectrophotometer (Finnigan MAT 252 Isotope Ratio Mass Spectrometer, Thermo Fisher Scientific Inc., Waltham, MA, USA). Apart from $\delta^{13}C_{leaf}$, the carbon (C) and nitrogen (N) concentrations in bamboo leaves were also measured using the same instrument.

2.4 Statistical analysis

The experiments were performed under a completely randomized design (CRD) procedure. Means of morphological (Table 1) and physiological characteristics (Table 5), of each species, were subjected to t-test for mean separation *(*significant level <0.05*)*. Normality of the culm size distribution *(*Figure 3*)* was tested for by the Shapiro-Wilk test using SigmaPlot software *(*Version 11.0, Systat Software Inc., San Jose, CA, USA*)*, at a significant level of < 0.05, to indicate that the data varies significantly from the pattern expected if the data was drawn from a population with a normal distribution. Linear regression technique was applied to determine the relationship between g_s and LAVPD. The magnitude of the slopes (Figure 4) was compared to test the differences in behavior, using the GLM procedure (SAS version 9.0; SAS Institute, Cary, NC, USA*)*. The estimate statement was used to test the slope difference *(*significant level <0.05*)*, as it enables the evaluation of a linear function of the parameters.

3. Results and Discussion

Carbon storage in plants can regulate carbon dioxide in the atmosphere and help with climate change issue. In this study, the ability of both bamboos to store carbon was studied, with other physiological factors. A total of 1002 (Thai bamboo) and 622 (Pai Liang) culms within an area of 7900 m^2, were assessed. The total density of Monastery bamboo was 0.13 culms m^{-2} while it was 0.08 culms m^{-2} for Pai Laing with the latter being slightly bigger in size than Monastery bamboo. As a result, the culm thickness, internode length, and leaf size were significantly greater in Pai Liang ($P < 0.0001$) (Table 1). Size class distribution of both the species was approximately normal (Figure 3) with the majority of culms lying in the middle size bin, with a circumference of 10.0-11.5 cm and 12.0-14.5 cm in the Monastery bamboo and Pai Liang, respectively.

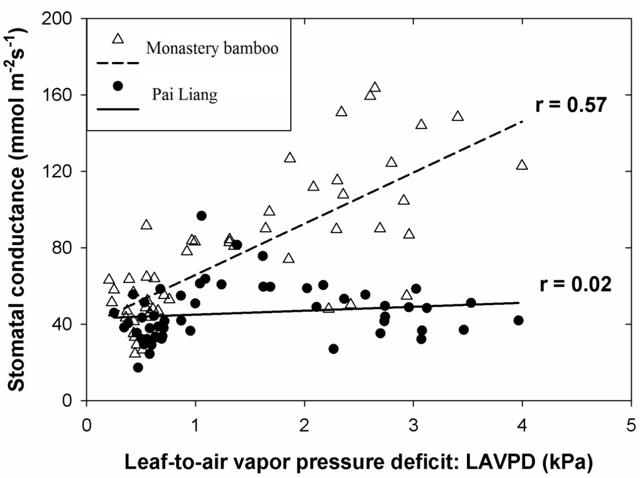

Figure 4. Scatter plot between leaf-to-air vapor pressure deficit (LAVPD) and stomatal conductance (g_s) for Monastery bamboo (open triangles) and Pai Liang (filled circles). The slopes of the two bamboo species were statistically different (P<0.0001), indicating different behavior of stomatal control over the ambient air gradient.

3.1 Dry biomass and carbon storage

Dry biomass and the subsequent carbon storage calculation were done using allometric technique. Possible allometric equations for dry biomass estimation based on DBH, total height, and the length of internode at 1.30 m are listed in Table 2 (Monastery bamboo) and Table 3 (Pai Liang). The best-fit equation for both the bamboo species was a function of $DBH^2 \times$ Total height. The allometric equation with DBH^2 as an independent variable was the next best fit and had a more simplistic form and ease of measurement. Therefore, it was equation chosen in this study (bold face equations in both the tables) for dry biomass and carbon storage calculations. The total dry biomass and carbon storage amounts in each culm of both the species are presented in Table 4 which indicates that the two quantities were close in value to each other. But carbon storage per culm was almost two times higher in Pai Liang as compared to the Monastery bamboo (last column, Table 4).

3.2 Physiological responses to microclimate

Stomatal conductance (g_s) is sensitive to the microclimate, especially air temperature and humidity. g_s in Pai Liang was almost two times lower than in Monastery bamboo (average of 45.9±1.9 vs. 75.84.7 mmol $m^{-2}s^{-1}$) (Figure 4). Leaf temperatures of both the species were not statistically different (P=0.645) with the mean leaf temperature of 30.0±3.9°C and 30.3 3.9°C in Monastery bamboo and Pai Liang, respectively. Leaf temperature in the rainy season was lower than in the summer season in both the species (27°C vs. 33°C). The ambient air temperature was 1-3°C higher than leaf temperature. LAVPD, which directly affects the stomatal aperture, ranged between 0.2-1.0 kPa (rainy season) and 1.0-4.0 kPa (summer season). In a combined dataset of both the seasons, Pai Liang maintained a stomatal aperture during all seasons while Monastery bamboo opened more stomata during the summer season, when the air was drier (high LAVPD) than usual. Chlorophyll content, which directly relates to photosynthesis was not statistically different in both species (P=0.753) (Table 5). This result can imply that the quantity of chlorophyll per unit area for photosynthetic process in both the species was not different.

WUE was presented as a carbon isotopic composition ($\delta^{13}C_{leaf}$), with a higher (less negative) number indicating a higher WUE. $\delta^{13}C_{leaf}$ in Pai Liang was significantly greater (less negative) than in Monastery bamboo (Table 5), indicating a better WUE in Pai Liang when compared to Monastery bamboo. Carbon content in Pai Liang leaves was higher than in Monastery bamboo, indicating that more carbon was stored in Pai Liang leaves. Nitrogen (N) content was not statistically different between both species suggesting that the N uptake rate of both species was similar. Since N is the main component of chlorophyll, the results matched the chlorophyll study here, in which both N and chlorophyll content were not significantly different (Table 5).

Pai Liang in this study area was a faster growing species (relative to Monastery bamboo) and in turn, stored more carbon in the tissue compared to the Monastery bamboo, as indicated by the carbon storage in each culm (last column in Table 4). The difference in growth of the two species could have resulted from differences in physiological behavior, with the stomata responded contrastingly to microclimate (Figure 3) leading to differences in WUE (Table 5). Monastery bamboo tended to lose more water due to greater stomatal aperture (Figure 4), even when the air dryness increased (high LAVPD). Previous studies found that the stomata of the rain forest tree species (Choat *et al.*, 2006; Heath, 1998; Maroco *et al.*, 1999) and also in grasses (Family Poaceae, also the bamboo family) (Leksungnoen *et al.*, 2012) closed as LAVPD increased, in order to prevent water loss. However, in this study, Monastery bamboo behaved differently from most species by opening its stomata more at high LAVPD (Figure 4). Even though this result is uncommon, some beech trees in mesic forests show similar behavior, due to the acclimation of hydraulic conductance to changing atmospheric evaporative demand (Uemura *et al.*, 2004). Monastery bamboo can be considered as an aggressive water use species (drought avoiding species) that would continue using water until there is no water supply, but it runs the risks of cavitation damage if a prolonged drought occurs (Kjelgren *et al.*, 2009). In contrast, Pai Liang's stomata were insensitive

Table 5. Physiological characteristics in the leaves of Monastery bamboo and Pai Liang including chlorophyll content (SPAD), WUE estimated as carbon isotopic composition (δ^{13}Cleaf) (‰), carbon (%), and nitrogen (%) content.

Species	Chlorophyll content ± SE (SPAD)	δ^{13}Cleaf ± SE (‰)	%C ± SE	%N ± SE
Monastery bamboo	43.13 ± 3.37NS*	-32.6 ± 0.72 b	39.8 ± 0.02 b	2.9 ± 0.002NS
Pai Liang	43.05 ± 4.06NS	-30.8 ± 0.58 a	42.4 ± 0.01 a	3.0 ± 0.020NS
P-Value	0.753	< 0.0001	< 0.0001	0.276

* Means with the different letters in the column were statistically different at significance level of P-value < 0.05. NS means no statistical difference between the mean of two bamboo species. SE is standard error.

to dry air, indicated by maintaining a stomatal aperture at the same rate over the LAVPD range. Similar behavior of some grass species (*Dactyloctenium aegyptium* and *Eragrostis tremula*), which are considered as drought escaping species, also shows independence of g_s on LAVPD (Maroco *et al.*, 1997). In this study, Pai Liang was superior in WUE than Monastery bamboo due to its ability to retain more water in the tissues (less water loss).

A large amount of chlorophyll would lead to more assimilation of carbohydrates and a higher WUE (Buttery & Buzzell, 1977; Peng *et al.*, 2011). In this study the amount of chlorophyll per unit area in both species was similar (Table 5). There should be some other physiological traits that contributed to the difference in growth of the two species. WUE would be the answer in this study. The differences in WUE between both the species was mainly due to the rate of water loss via stomata rather than a faster rate of photosynthesis. However, Pai Liang had more leaf area than Monastery bamboo (more leaf dry biomass as indicated in Table 1) which led to greater total amount of chlorophyll in Pai Liang. As a result, Pai Liang produced more photosynthate and a faster growth (Table 1) compared to Monastery bamboo. Nitrogen is the main component of chlorophyll which directly affects the photosynthetic rate and enhances WUE by increasing the assimilation rate (Ripullone *et al.*, 2004), via nitrogen investment in the photosynthetic process with no influence on stomatal aperture (Verlinden *et al.*, 2015). In this study, nitrogen percentage (related to chlorophyll content), was not statistically different between both species (Table 5). Better growth, a greater leaf area, and more carbon storage in Pai Liang resulted from a more wise use of water compared to Monastery bamboo.

Considering the climate change mitigation on a global scale, Pai Liang is recommended not only owing to its relatively rapid growth rate but also because of greater carbon storage in the culm, which was twice of what the Monastery bamboo could store. Pai Liang has a great potential to remove carbon dioxide from the atmosphere and mitigate climate change, because the amount of carbon storage at around 1.328 kg C per culm is relatively similar to other bamboo species in previous study; 0.04-1.823 kg C per culm in bamboo forest in China (Zhou *et al.*, 2011); 2.38 kg C per culm in natural mixed deciduous forest of Thailand (Chaiyo *et al.*, 2012); 2.35 kg C per culm of Makino bamboo in Taiwan (Yen *et al.*, 2010); 14 kg C of carbon per culm of Moso bamboo in China (Zhuang *et al.*, 2015). Additionally, both the natural and plantation bamboo have a wide range of carbon storage per hectare from 10-90 tons C ha^{-1} which is considered as a good source of carbon sink, when compared to the mixed deciduous and dry every green forests that can store 48 and 70 tons C ha^{-1}, respectively (Terakunpisut *et al.*, 2007).

4. Conclusions

Pai Liang shows better growth and more stored carbon than Monastery bamboo due to a better WUE. Monastery bamboo lost more water from opening its stomata even when the air became dry. Pai Liang maintained a low stomatal aperture in order to conserve water within its tissues. There was no difference in chlorophyll content, suggesting that the photosynthetic rate of both species could be similar, but since Pai Liang had more leaf area, it was superior at assimilating while losing less water compared to Monastery bamboo. Unlike Pai Liang, Monastery bamboo lost more water during the photosynthesis process leading to a lower WUE and subsequently, a relatively lower growth rate. In a climate change scenario, Pai Liang is recommended from a commercial and environmental stand point, owing to greater carbon fixation and rapid growth rate compared to the Monastery bamboo.

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