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The ecological adaptability of four typical plants during the early successional stage of a tropical rainforest

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Abstract
The ecological adaptability of four typical plants (two grasses: *Thysanolaena maxima* and *Miscanthus floridulus*; two shrubs: *Melastoma candidum* and *Melastoma sanguineum*) in the early successional stage of a tropical rainforest in Hainan Island of China was studied. Our purpose was to test the difference of the adaptive modes and ecological functions for four different functional groups. We measured the physiological parameters and morphological indexes to define the adaptability of the plants at this stage. Results showed that *T. maxima* possessed stronger water use ability, whose adaptation was mainly by the morphological architecture regulation strategy (by higher leaf self-shading). *M. floridulus* had greater water regulation ability and its adaptation was mainly through the physiological regulation strategy (by higher net photosynthetic rate (A) and water use efficiency). However, *M. candidum* and *M. sanguineum* integrated the morphological architecture and physiological strategies (by high A and leaf self-shading). According to the ecophysiological characteristics and adaptation modes, the plants in the early successional stage of the tropical rainforest in Hainan Island can be categorized into three functional groups: (1) physiological adaptation group, (2) morphological adaptation group, and (3) physiological and morphological integrated adaptation group.

Keywords: *Ecological adaptation, functional group, morphological architecture, photosynthetic characteristics, water availability*

Introduction

Ecological succession is an interacting complex of processes, accompanying the continuous changes of community energetics, structure, life history, nutrient cycling, selection pressure, and overall homeostasis (Odum 1969). In the early stages of ecological succession, the energy and biomass of ecosystem increase quickly, and the physical environments of plants improved step by step until it fit the later species (Odum 1969; Maestre et al. 2001). However, in the early successional stage, living environments are difficult for plants to survive due to excessive light, lack of water, and scarce nutrient in the soil (García-Orth & Martínz-Ramos 2011). But the vast energy fixing by plants through strong photosynthetic capacity (Navas et al. 2010), root growth (Maestre et al. 2001, 2009), and litter decomposition (Wardle et al. 1998; Maestre et al. 2001) improves the habitat and accelerates the process of plant succession to a certain extent. Grasses can ameliorate the abiotic environment and facilitate the introduction of other species. However, shrubs show stronger effect on improving habitat conditions (Maestre et al.

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2009; Cuesta et al. 2010) and attracting more seed dispersers (Hooper et al. 2005) than grasses, which play a more significant function in facilitating forest regeneration (Cuesta et al. 2010; Celis & Jose 2011; García-Orth & Martínz-Ramos 2011; Ortega-Pieck et al. 2011).

Plants in open environments are exposed to high irradiance, which frequently leads to not only photoinhibition (Long et al. 1994) but also high temperature, heat, and water deficit. In low temperature conditions, excessive solar radiation leads to more serious damage to plant performances (Bader et al. 2007; Vitale & Santo 2008). Under these circumstances, plants exhibit two general strategies: one physiological and the other structural or architectural. However, plants often combine these two strategies with different emphasis on each depending on the species and the environmental conditions (Valladares 1999). In the first strategy, the photosynthetic units are protected against excessive light intensity by physiological and biochemical processes, which involve photochemical reaction (CO_2 assimilation, photorespiration, and Methler reaction) and xanthophyll-dependent thermal dissipation (Murchie & Niyogi 2011). In this stage, plants have high-photosynthetic capacity (Navas et al. 2010), which is an important manner of using plenty of light energy through high-photosynthetic rate (Medrano et al. 2002). With increase in light intensity, air temperature increases whereas humidity decreases. Plants can improve transpiration rate by regulating stomatal conductance to maintain leaf temperature to an appropriate physiological extent (Larcher 1995; Nicotra et al. 2008). Excessive light, often occurring with high-leaf temperature or water deficit, is a major environmental stress leading to midday depression of photosynthesis (Valladares & Pearcy 1997). Cowan (1982) suggested that increase of transpiration demand lead to decrease of stomatal conductance and CO_2 assimilation (Mott & Parkhurst 1991). Because stomatal closure decreases photosynthetic rate, the photorespiration rate correspondingly increases with a decreasing CO_2:O_2 ratio, consuming plenty of light energy (Muraoka et al. 2000; Medrano et al. 2002). When the rate of photosynthesis reaches saturation, production of reactive oxygen species in the photosynthetic apparatus will increase due to absorbption of excess light (Li et al. 2009). The primary mechanism of plant leaves countering the increase of reactive oxygen species is by enhancing the activity of a complex of constitutive antioxidant enzymes (Guidi et al. 2008; Foyer & Shigeoka 2011).

It has been shown that plant structural avoidance of excessive irradiance may be crucial for survival under extreme conditions (Valladares & Pearcy 1997; Muraoka & Koizumi 2005). Photosynthetic photo flux density (PFD) intercepted on a leaf surface area is reduced by the change of the architecture of plants (Valladares & Pearcy 1998; Pearcy et al. 2005). In high-light environments, leaf angle and self-shading provide structural photoprotection, minimizing potential damage from photoinhibition (Pearcy et al. 2005). For relatively simple canopies, leaf angle and orientation are the main structural photoprotective features (Muraoka & Koizumi 2005), but mutual shading among leaves can be even more important in complex, multilayered canopies (Ramírez et al. 2008). Because of being more exposed to excessive light, outer layers of the canopy suffer more drastic changes in the abiotic conditions than inner layers (Niinemets 2007). Plant leaves show different ecophysiological traits at different positions in the canopy (Casas et al. 2011; Giorio & Nuzzo 2012). Without these structural protections, photoinhibition of photosynthesis is likely to be much greater, which leads to apparent reduction of daily carbon gain (Pearcy et al. 2005).

Recently, terrestrial plant ecologists have revived the idea of a functional classification in order to predict possible changes in the vegetation as a result of global climate change (Lavorel et al. 1997). Smith et al. (1993) coined the term "plant functional types", and Gitay and Noble (1997) defined it as "set of species showing similar responses to the environment and similar effects on ecosystem function". There have been some researches on plant functional groups (Wardle et al. 1998; Gebauer et al. 2002; Reich et al. 2003; Hanley et al. 2004; Chen et al. 2005; Golluscio & Oesterheld 2007; Letts et al. 2010; Kamiyama et al. 2010). The usual groupings are defined by discrete and measurable biological trait differences (e.g., whether a plant fixes nitrogen or not, has perennial woody tissues or not, and has a given photosynthetic pathway or not) (Reich et al. 2003). Lavorel et al. (1997) considered that classifications could not be expected to be universal, yet their development should aim at reaching greater generality by addressing mechanism. However, as information on plant traits and their relationship with climate have increased during the last decade (Wright et al. 2004), functional group classification on a global scale is becoming possible based on plant trait distribution against bioclimatic variables, whereas the central challenge is how to define a short list of observable and quantitative traits (Harrison et al. 2010). Notwithstanding, few classifications of plant functional groups have been based on plant function for briefly knowing about the relationship between forms and functions.

The tropical rainforest in Hainan Island of China is one of the most important forest ecosystems with the most complex structure and the richest biodiversity, possessing significant values of conservation

and research. However, excessive deforestation and unreasonable land use have led to a large reduction of primary forest area and formed degraded ecosystems of different successional stages. The natural secondary forest, which developed after the primary forest was destroyed, is the most important forest resource in Hainan Island (Zang et al. 2004). Because the tropical rainforest has suffered severe damages, considerable areas of degraded tropical forests in Hainan Island are in the early successional stage of recovery. A study on the vegetation of this early recovery stage not only increases our knowledge of the successional mechanism of the tropical rainforest but also has some implications for the management and restoration of degraded ecosystems in tropical regions.

In this study, we selected four typical plant species (two grasses and two shrubs) to study their adaptabilities and ecological functions during the early successional stage of recovery in a tropical rainforest of the Jianfengling forest region in Hainan Island, South China. Here, we define the early successional stage as the stage dominated by grasses/shrubs. The four typical plant species (two grasses: *Thysanolaena maxima* and *Miscanthus floridulus*; two shrubs: *Melastoma candidum* and *Melastoma sanguineum*) are the most occurring species in the early successional stages of Hainan Island. We measured the natural microclimatic factors around the plants and the physiological and morphological characteristics of the plants in order to discuss the following two questions: (1) How the plant species adapt to the early successional physical environment? (2) Whether the plants in the early successional stages of recovery can be categorized into different functional groups according to their physiological/morphological characteristics and adaptive modes?

Materials and methods

Study site

The study was carried out at the Jianfengling Long-Term Ecological Research Station in Hainan Island, China (latitude 18°44′N, longitude 108°55′E, altitude 820 m). Jianfengling region experiences a tropical monsoon rain climate. Mean annual rainfall is about 2651 mm and mean annual air temperature is 19.7°C with a distinct wet season between May and October (Luo et al. 2001). We selected an open belt of about 0.2 ha, where the vegetation was cleared for building roads but abandoned 6 years ago. The extant vegetation is predominantly grasses and shrubs, occasionally the seedlings of pioneer trees such as *Sapium discolor* (Champ. Ex Bench.) Muell.-Arg., and *Endospermum chinense* Benth. Fl. Hongk. could be found, and no shade-tolerant trees appeared. The dominant grass species are *T. maxima* (Roxb.) Kuntze. and *M. floridulus* (Labill.) Warb.ex Schum. et Lauterb., and the dominant shrubs are *M. candidum* D.Don and *M. sanguineum* Sims. *T. maxima* and *M. floriadulus* (Poaceae) distributed broadly (Guangdong Institute of Botany 1977), and *M. candidum* and *M. sanguineum* (Melastomataceae) exist mainly in open areas (Chun 1965). The four dominant species in the early successional stage were studied in the field in this paper.

Measurements of microhabitat and physiology

Leaf gas exchange measurements were made every 2 h from 8:00 to 18:00 h for three clear days in the dry season in April 2006. We measured in two mature leaves in fine sun from the top of the canopy in each of the 10 plants of a species. Gas exchange was measured with an open portable photosynthesis system (LI-6400; Li-COR Inc., Lincoln, NE, USA). During gas exchange measurements, the plants had been receiving full sunlight. We measured PFD, atmospheric temperature (T_a), relative humidity (R_h), net photosynthesis rate (A), stomatal conductance (g_s), transpiration rate (E), and leaf temperature (T_l). Instantaneous water use efficiency (WUE) was calculated as the photosynthetic carbon assimilation (A) per unit of transpiration (E).

Measurements of morphology

The seedlings of 10 *T. maxima*, 30 *M. floriadulus*, 10 *M. candidum*, and 10 *M. sanguineum* were excavated randomly by hand to recover as many roots as possible in the field. The harvested grass seedlings were partitioned into above-ground and root parts, and shrub seedlings were partitioned into stem, leaves, and roots, dried at 75°C to a constant weight and weighed to the nearest 0.01 g. Leaf area of individual leaves each species was measured with a Li-COR LI-3000A portable area meter. Leaf area: total plant biomass ratio (LAR), leaf area index (LAI), root mass:total plant biomass ratio (RMR), and root:shoot ratio (RS) were recorded for each harvested plant.

Data analysis

Physiological (mean daily value of A, g_s, E, T_l, and WUE) and morphological (LAR, LAI, RMR, and Rs) indexes were tested by one-way ANOVA. The statistically significant was set at $P < 0.05$. We analyzed nine traits by principal component analysis (PCA): five physiological indexes (mean daily value of A, g_s, E, T_l, and WUE) and four morphological parameters (LAR, LAI, RMR, and

Rs). All statistics were calculated with SPSS for Windows 13.0 (SPSS, Chicago, IL, USA).

Results

Diurnal changes of A, g_s, E, T_l, and WUE

T. maxima, *M. candidum*, and *M. sanguineum* had the maximum *A* at 8:00 h and then decreased during the day (Figure 1). However, *A* of *M. floriadulus* showed a unimodal curve, and the maximum was at 10:00 h. *M. floriadulus* had the higher *A* than *T. maxima*, *M. candidum*, and *M. sanguineum*. g_s varied slightly in the day, *T. maxima* and *M. floriadulus* had lower g_s than *M. candidum* and *M. sanguineum*. *E* was bimodal pattern for *T. maxima*, the peak value appeared at 12:00 and 16:00 h, respectively. However, *E* showed a midday peak for *M. floriadulus*, *M. candidum*, and *M. sanguineum*; it reached the maximum at 12:00 h. *E* was lower for *T. maxima* and *M. floriadulus* than for *M. candidum* and *M. sanguineum*. The diurnal pattern of T_l displayed a unimodal, reaching the peak value at 10:00 h for *T. maxima* and *M. sanguineum*, and it was at 12:00 h for *M. floriadulus* and *M. candidum*. T_l was close among the four species. At 8:00 h, WUE for the four species was the greatest but declined obviously at 10:00 h and then changed gently. In the four species, the order of WUE was *M. floriadulus* > *T. maxima* > *M. candidum*, and *M. sanguineum*.

There were significant differences among the four species on the mean daily *A* ($F = 3.57$,

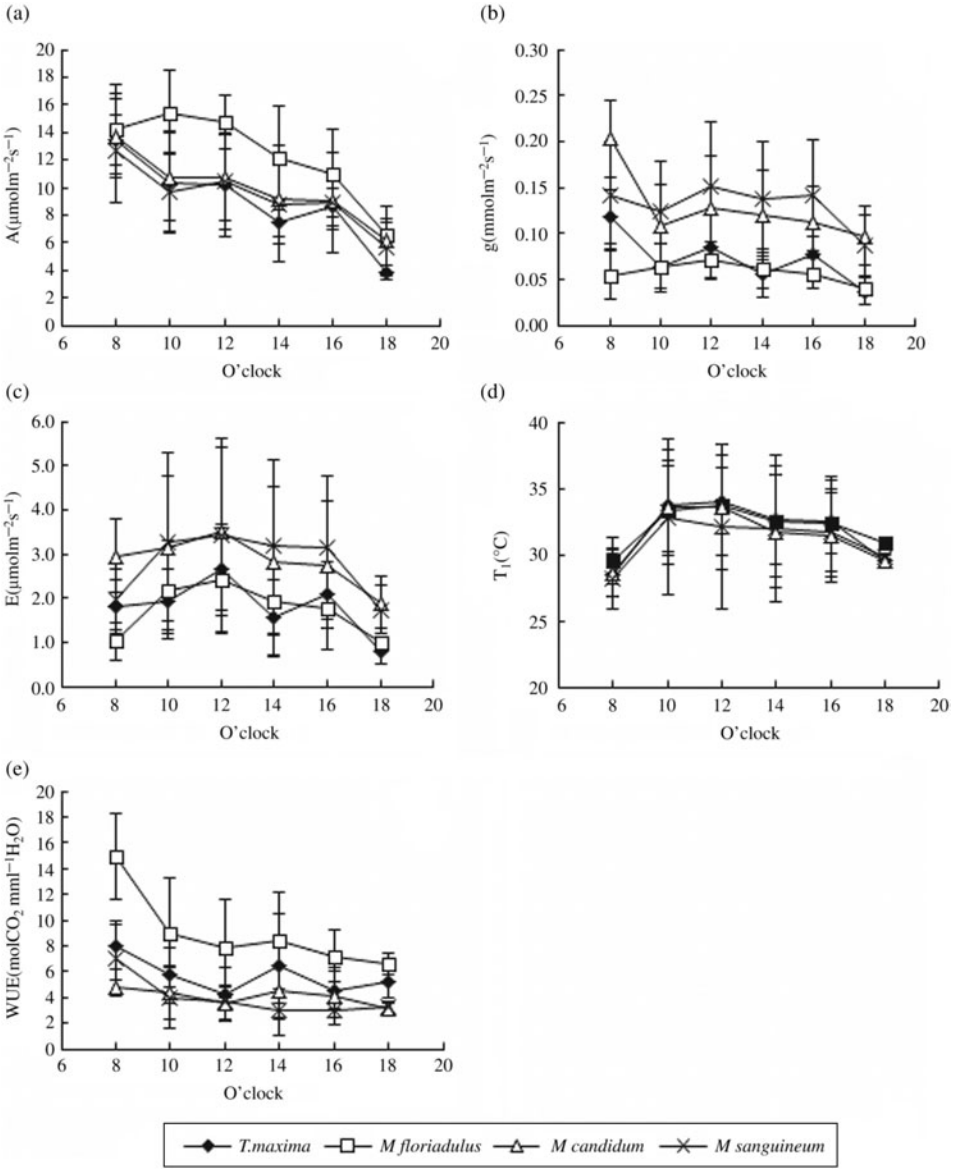

Figure 1. (a) Diurnal changes of net photosynthetic rate (*A*), (b) stomatal conductance (g_s), (c) transpiration rate (*E*), (d) leaf temperature (T_l), and (e) WUE of the four species.

Table 1. Regression equations describing relationships among net photosynthesis rate (A), stomatal conductance (g_s), leaf temperature (T_l), and photosynthetic PFD for the four species.

Species	Regression equation	R^2-value	P-value
T. maxima	$A = 75.434g_s + 3.593$	0.577	$P < 0.01$
	$A = -0.407T_l + 22.221$	0.161	$P < 0.01$
	$g_s = -0.004T_l + 0.197$	0.141	$P < 0.01$
	$A = -1.2E-5\text{PFD}^2 + 0.020\text{PFD} + 4.518$	0.596	$P < 0.01$
M. floridulus	$A = 122.979g_s + 5.569$	0.481	$P < 0.01$
	$A = 0.517T_l - 3.328$	0.228	$P < 0.01$
	$g_s = 0.003T_l - 0.031$	0.211	$P < 0.01$
	$A = -5.6E-6\text{PFD}^2 + 0.015\text{PFD} + 5.476$	0.499	$P < 0.01$
M. candidum	$A = 41.440g_s + 4.484$	0.408	$P < 0.01$
	$A = -0.122T_l^2 + 7.986T_l - 118.219$	0.137	$P < 0.01$
	$g_s = -0.006T_l - 0.321$	0.186	$P < 0.01$
	$A = -9.7E-6\text{PFD}^2 + 0.019\text{PFD} + 4.464$	0.332	$P < 0.01$
M. sanguineum	$A = 28.913g_s + 5.724$	0.204	$P < 0.01$
	$A = -0.060T_l^2 + 4.030T_l - 56.631$	0.095	$P < 0.01$
	$g_s = -0.005T_l + 0.294$	0.173	$P < 0.01$
	$A = -7.7E-6\text{PFD}^2 + 0.017\text{PFD} + 2.794$	0.310	$P < 0.01$

$P < 0.05$), g_s ($F = 55.67$, $P < 0.01$), E ($F = 5.49$, $P < 0.01$), and WUE ($F = 25.13$, $P < 0.01$), except, for the mean daily T_l ($F = 0.23$, $P = 0.88$). The mean daily A ($P < 0.01$) and WUE ($P < 0.01$) for *T. maxima* were obviously lower than for *M. floriadulus*, but the mean daily g_s ($P = 0.10$) and E ($P = 0.99$) for them were not significant. There were no significant differences between *M. candidum* and *M. sanguineum* on the daily mean of A ($P = 0.49$), g_s ($P = 0.30$), E ($P = 0.98$), and WUE ($P = 0.79$). *M. candidum* and *M. sanguineum* were similar to *T. maxima* ($P = 0.16$ and $P = 0.56$, respectively) on the mean daily A, but lower than *M. floriadulus* ($P < 0.05$). Moreover, *M. candidum* and *M. sanguineum* had higher mean daily g_s ($P < 0.01$) and E ($P < 0.05$) and lower WUE ($P < 0.01$) than *T. maxima* and *M. floriadulus*.

The relationships among A, g_s, T_l, WUE, and PFD

There were significant positive correlations between A and g_s (Table 1). The regression coefficients of *T. maxima* and *M. floriadulus* were higher than those of *M. candidum* and *M. sanguineum*, which indicated that *T. maxima* and *M. floriadulus* were more sensitive than *M. candidum* and *M. sanguineum*.

With an increase in T_l, A of *T. maxima* decreased, A of *M. floriadulus* increased, and A of *M. candidum* and *M. sanguineum* increased in a significant quadratic polynomial way (Table 1). However, as T_l increases, g_s of *T. maxima*, *M. candidum*, and *M. sanguineum* decreases, but g_s of *M. floriadulus* increases (Table 1).

As PFD increases, A increases in a significant quadratic polynomial way for the four species (Table 1). According to the regression equations, PFD at the maximum A was 849.49 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for *T. maxima*, 1339.39 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for *M. floriadulus*, 963.83 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for *M. candidum*, and 1127.39 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for *M. sanguineum*.

Morphological indexes of the four species

Plant morphological construction is an important value for them to adapt to the living environments. For the four species, LAI ($F = 23.33$, $P < 0.01$) and LAR ($F = 8.28$, $P < 0.01$) differed significantly ($P < 0.01$), but Rs ($F = 0.67$, $P = 0.58$) and RMR ($F = 1.79$, $P = 0.16$) showed no obvious differences, which indicated that their morphological construction was similar to a certain extent in high-light environment. LAR was similar in *T. maxima* and *M. floriadulus* ($P = 0.66$), which was higher in

Table 2. Root:shoot ratio, root biomass:total plant mass ratio, leaf area ratio, and leaf area index of the four species (mean ± SD).

Species	Rs	RMR	LAR ($\text{cm}^2\,\text{g}^{-1}$)	LAI
T. maxima	$0.48^a \pm 0.04$	$0.28^a \pm 0.08$	$51.51^{ABa} \pm 14.92$	$0.99^{Aa} \pm 0.33$
M. floridulus	$0.53^a \pm 0.04$	$0.34^a \pm 0.02$	$48.60^{Aa} \pm 13.59$	$0.32^{Bb} \pm 0.02$
M. candidum	$0.45^a \pm 0.12$	$0.29^a \pm 0.01$	$31.99^{BCa} \pm 6.77$	$0.60^c \pm 0.09$
M. sanguineum	$0.48^a \pm 0.07$	$0.31^a \pm 0.05$	$28.32^{Ca} \pm 8.46$	$0.53^c \pm 0.04$

Notes: Values followed by different letters are significantly different from each other. Lowercase letters denote significance at $P < 0.05$ level and uppercase letters at $P < 0.01$ level.

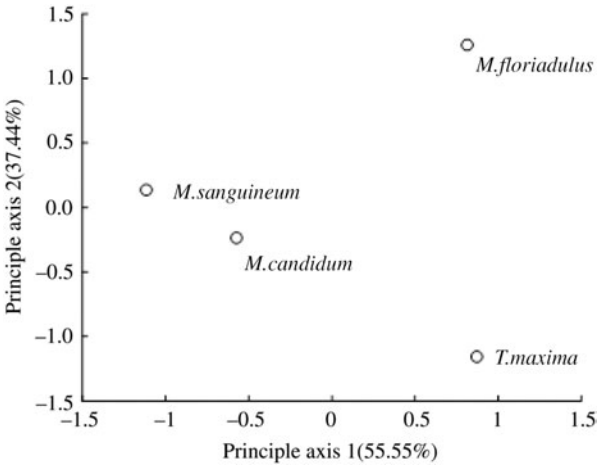

Figure 2. Plots ordination of PCA in the four species.

M. candidum and *M. sanguineum* ($P < 0.05$), whereas, it was similar in *M. candidum* and *M. sanguineum* ($P = 0.57$). *T. maxima* had the greatest LAI, then had *M. candidum* and *M. sanguineum*, and *M. floriadulus* had the least (Table 2).

Principal component analysis

We analyzed nine traits by PCA: five physiological indexes (mean daily value of A, g_s, E, T_l, and WUE); four morphological parameters (Rs, RMR, LAR, and LAI), and the first two principal components were used to do the analysis (Figure 2). The first two axes included 92.99% of the variation. The greatest amount of variation (Axis 1, 55.55%) was associated with species' ability of controlling water (mean daily value of g_s, E, T_l, WUE, and LAR). The second axis (Axis 2, 37.44%) was associated with species' ability of photosynthesis, including A, LAI, RMR, and Rs. The results via PCA showed that the plants in the early successional stage of tropical forest recovery could be divided into three groups: (1) the first group, represented by *T. maxima*, possessed stronger water use ability, lesser photosynthetic capacity, and greater self-shading of the leaves; (2) the second group, represented by *M. floridulus*, possessed stronger water use ability, greater photosynthetic capacity, and lower self-shading of the leaves; and(3) the third group, represented by *M. candidum* and *M. sanguineum*, had lower water use ability, moderate photosynthetic capacity, and moderate self-shading of the leaves.

Discussion

We found that grasses and shrubs had different physiological adaptive modes. High irradiance usually led to photoinhibition for plants surviving in open environments (Long et al. 1994). A of the four species suffered from depression in different degrees under higher irradiance. According to the PFD at the maximum A, *T. maxima* suffered the most severe inhibition during the diurnal changes, the next was *M. candidum* and *M. sanguineum*, and the last was *M. floridulus*. High irradiance also leads to higher leaf temperature. When T_l exceeds the normal physiological temperature range, leaf physiology will be limited (Valladares & Pearcy 1997). The increase in T_l led to the most serious inhibition on photosynthetic physiology for *T. maxima*, then for *M. candidum* and *M. sanguineum*. However, *M. floridulus* benefited from the increase of T_l. So, in the early successive stage, *T. maxima* suffered the most severe stress on photosynthetic physiology, and then was *M. candidum* and *M. sanguineum*. However, *M. floridulus* could acclimate to high irradiance successfully by higher photosynthetic capacity. For two grasses, *T. maxima* were similar to *M. floridulus* in g_s and E. However, *T. maxima* had lower A than *M. floridulus*. Plants can consume considerable light energy to avoid excessive radiation and destroy the photosynthetic units by higher photosynthetic capacity (Medrano et al. 2002). So higher photosynthetic capacity was one of the important adaptive modes for *M. floridulus*. *T. maxima* perhaps had other adaptive patterns. In Hawaiian dry forest, the dominance of fountain grass may not be due to superior photosynthetic attributes than other species (Cabin et al. 2002). Two shrubs, *M. candidum* and *M. sanguineum*, had higher g_s and E than *T. maxima* and *M. floridulus*. Plants can keep normal leaf physiological temperature through regulating g_s to control E (Larcher 1995). With an increase in T_l, g_s of *M. candidum* and *M. sanguineum* decreased more quickly than that of *T. maxima* and *M. floridulus*, indicating that shrubs had stronger adjusting capacity than grasses on stomata (Letts et al. 2010). The profligate water use of shrubs is related to their deeper rooting systems (Gebauer et al. 2002; Chen et al. 2005; Letts et al. 2010).

Water use strategies of plant species may partially explain the differences in plant composition and competitive ability of co-existing species. Compared with shrubs, some studies thought that grasses were profligate (Golluscio & Oesterheld 2007; Letts et al. 2010), but others thought that they were conservative (Gebauer et al. 2002; Chen et al. 2005). Profligate water use of grasses conduced to inhibit shrub growth by reducing soil moisture rapidly within their rooting depth (Golluscio & Oesterheld 2007; Letts et al. 2010). However, high efficiency in the use of water is vital for plants to survive in the open environment; especially, most of the tropical rainforests usually experience very high water stress during the dry season (Valladares & Pearcy 1997). *T. maxima* and *M. floridulus* possessed higher WUE than *M. candidum*

and *M. sanguineum*, which was similar to the research in the Xilin River Basin, Inner Mongolia, China (Chen et al. 2005) and in the northern Chihuahuan Desert grassland (Throop et al. 2012). Shrubs generally have deeper root systems than grasses (Letts et al. 2010). Because of constant water resources in deeper soil layer, shrubs use a relatively prodigal water use pattern (Gebauer et al. 2002; Chen et al. 2005; Pochman & Small 2010).

However, only physiological adaptation is not enough, plants need to regulate adaptation by morphological architecture correspondingly. Under full sunlight conditions, architecture plays the important fundamental role as the defense against temperature extremes and photoinhibition through avoidance of excessive radiation loads on the leaf surfaces (Valladares & Pearcy 1998; Pearcy et al. 2005). The four species were similar in RMR and Rs, indicating that no significant differences were shown in root biomass invested between grasses and shrubs. However, some researches showed that grasses had greater specific root length than shrubs (Leonard et al. 2008). Thereby, root traits of grasses and shrubs need to strengthen research. *T. maxima* and *M. floridulus* exhibited higher LAR than *M. candidum* and *M. sanguineum*, which was related to the increase in stem mass investment for shrubs (Hunt & Cornelissen 1997; Kamiyama et al. 2010). Plant growth is strongly dependent upon LAR (Hunt & Cornelissen 1997). Higher LAR of grasses favors their fastest above-ground growth and the formation of leaf layers, decreasing the light interception by short shrubs (Aerts et al. 1991). Plants achieve their maximum daily carbon gain by leaf angle and self-shading, providing structural photoprotection, minimizing potential damage from photoinhibition in high-light environments (Valadares & Pearcy 1998; Ramírez et al. 2008). *T. maxima* had the greatest LAI, the next was *M. candidum* and *M. sanguineum*, and the least was *M. floridulus*, indicating that *T. maxima* made the most use of leaves self-shading, *M. candidum* and *M. sanguineum* were in the middle, and the least was *M. floridulus*. Under tall and dense grass, light level was too low for shrubs and tree seedlings to regenerate (Celis & Jose 2011; Ortega-Pieck et al. 2011). Therefore, tall and dense *T. maxima* can hamper introducing shrubs and tree seedlings.

Plants exposed to high light often combine physiological and architectural strategies, but with different emphasis on each, they depend on the species and the environmental conditions (Valladares 1999). Combining the physiological and morphological indexes of the four species, the adaptive modes of the four species were very different in the high-light environments. After examining the traits measured in this study by PCA, according to their adaptive modes, the four species could be divided into three groups. *T. maxima* possessed stronger water use ability, with more emphasis on morphological architecture strategy, maximized A and mastered E and T_l through leaf changes (rolling in clear day and spreading in the overcast day) and self-shading. *M. floridulus* provided greater water use ability emphasizing more on the physiological strategy (photosynthetic capacity), which was the most responsible manner, and higher WUE was vital for it to survive. However, *M. candidum* and *M. sanguineum* integrated the morphological architecture and physiological strategies, with higher leaves self-shading in architecture and A and E in physiology. *T. maxima* and *M. floridulus* had greater water use ability than *M. candidum* and *M. sanguineum*, which indicated that herbaceous plants possessed stronger survival capacity than shrubs in the early successional stage (Mahall & Schlesinger 1982).

Because of the difficulty in measuring functional traits experimentally and specific research aims, few plant functional classifications have been based on functional traits, though it is the essential method. Although differences were significantly enough among trait-based functional groups, it did not effectively discriminate herbaceous species (Reich et al. 2003). Using mixtures of 14 calcareous grassland plant species drawn from three functional groups (nonleguminous forbs, grasses, and leguminous forbs), Hanley et al. (2004) concluded that because of the idiosyncratic responses of individual species, the categorization of plants into broad functional groups was of limited use to understand the impacts of elevated atmospheric CO_2 on plant communities. Moreover, plant species which were selected from the dicotyledonous herbs functional group had large difference between species for all of the ecophysiological traits measured (Wardle et al. 1998). In this paper, we also found significant differences in ecophysiological traits between grasses. This research showed that it was very difficult to divide plants into different functional groups because of remarkable difference in plant biological characteristics. We need to strengthen the research on plant biological characteristics and shortlist and reasonable traits that will be sufficient to characterize plant functional groups. According to the ecophysiological characteristics and adaptation modes of the four typical representative species' early successional stage of tropical rainforest in Hainan Island, we concluded that there existed three functional groups in the early successional stage of tropical rainforest in Hainan Island: (1) physiological adaptation group, represented by *M. floridulus*, possessed stronger water use ability, greater photosynthetic capacity, and lower self-shading of the leaves; (2) morphological adaptation group, represented by *T. maxima*,

possessed stronger water use ability, less photosynthetic capacity, and greater self-shading of the leaves; and (3) physiological and morphological integration adaptation group, represented by *M. candidum* and *M. sanguineum*, had lower water uptake ability, moderate photosynthetic capacity, and moderate self-shading of the leaves.

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