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Responses of clonal growth and photosynthesis in *Amomum villosum* to different light environments

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Abstract

Clonal growth is of great importance for survival, growth, expansion, and resource utilization of some species. Knowing how clonal plants respond morphologically and physiologically to different light environments can be useful to explain their occurrence and abundance patterns under specific environmental conditions. Responses of clonal growth, leaf gas exchange, fluorescence emission, and photosynthetic pigment concentrations to different light environments (100, 60, 30, and 15%) were studied in *Amomum villosum,* grown in the traditional way for economic purpose in Xishuangbanna, southwest China. The results showed that *A. villosum* attained vigorous clonal growth under 30% and 60% light, with a higher plant height, number of ramets, stolon length, thicker stems and stolons. Shade-grown *A. villosum* possessed a larger leaf area than that of the sun-grown plants in order to capture more light. For *A. villosum*, the higher light-saturated net photosynthetic rate, light-saturation point, larger fresh and dry biomass can explained the better clonal growth for *A. villosum* under 30% and 60% light. *Amomum villosum* attained the highest values of minimal chlorophyll fluorescence under 100% light and the lowest values of maximum photochemical efficiency of PSII under 15% light. Our findings indicated that the full irradiance was too strong and 15% light was too weak for *A. villosum* plants. It was also verified by higher concentrations of photosynthetic pigments in the shaded plants compared to those grown under full sun light. Our results suggested that *A. villosum* seemed to be adapted to moderate light environment (60–30%) which was indicated by vigorous clonal growth and higher photosynthesis. This information is very useful to select clonal species for rainforest or understory projects. The cultivation of *A. villosum* in rainforest should not be done under too strong (100%) or too weak light environment (less than 15%).

Aditional key words: gas exchange; leaf morphological traits; ramets; shade; stolon stretch.

Introduction

Clonal plants play an important role in community and ecosystem processes (Oborny and Bartha 1995). Clonal growth is also of great importance for the survival, growth, expansion, and resource utilization of some species, such as bamboo (Saitoh *et al.* 2002) and strawberry (Wilk *et al.* 2009). Clonal plant establishment is facilitated by vegetative growth and physiological integration. Clonal growth is characterized by the production of genetically identical descendants (ramets) and is very representative in most environments. In clonal plants, the incessant production of ramets on primary and lateral stolons allows the clone to spread horizontally. This may result in the formation of extensive clonal systems with many interconnected ramets scattered in space, so that they are likely to experience environmental heterogeneity (Roiloa and Retuerto 2007). Indeed, in most habitats, biotic,

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Abbreviations: Car – carotenoid; Chl – chlorophyll; FL – full sunlight; F_0 – minimal fluorescence yield of the dark adapted state; F_v/F_m – maximal quantum yield of PSII photochemistry; LCP – light-compensation point; LSP – light-saturation point; P_{Nmax} – light-saturated net photosynthetic rate; R_D – dark respiration rate; S15 – 15% shading ; S30 – 30% shading ; S60 – 60% shading; α – apparent quantum yield.
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climatic, and topographic factors show a striking degree of small scale heterogeneity (Lechowicz and Bell 1991, Jackson and Caldwell 1993). Although clonal integration generally confers advantages to ramets growing under less favorable conditions, phenotypic plasticity in clonal plants may improve their ecological adaptability (Dong 1995, Alpert 1999, Saitoh *et al.* 2002). It has been repeatedly documented that clonal growth brings about benefits (resource acquisition, successful establishment of offsprings in new environment, risk aversion for the genet) as well as costs (transmission of diseases, a decrease of resources available for sexual reproduction) to the plant (Klimeš *et al.*1997).

Of all the environmental factors affecting plants, light is perhaps the most significant factor affecting plant survival, growth, reproduction, and distribution. However, in any habitat, light varies in time and place and light intensity is extremely different and varied in the rainforest or understories, thus inducing plants to develop acclimation to the variation of light intensities (Zhang *et al.* 2003). Most plant species are able to acclimate to different light conditions by special acclimation and phenotypic plasticity (Hanba *et al.* 2002, Wyka *et al.* 2008). Acclimation to changing light conditions is achieved through adjustments at different levels. Moreover, in order to sustain higher photosynthetic capacity or survival, plants modify their morphology and biomass allocation under different light conditions. Clonal growth and leaves usually exhibit a remarkable capacity to adjust their morphology and physiology in response to different light conditions due to their phenotypic plasticity (Bond *et al.* 1999, Valladares *et al.* 2007, Yoshimura 2010). According to Ryser and Eek (Ryser and Eek 2000), the adaptive phenotypic plasticity differences among species may contribute to their different abilities to occupy variable and diverse habitats in the nature. Here, we focused on a question how clonal plants regulate their clonal growth and leaf morphological characteristics under different light environment. Knowing how plants respond morphologically and physiologically to different light environments can be useful to explain their occurrence and abundance patterns under specific environmental conditions.

Amomum villosum Lour. (Zingiberaceae), a famous medicine plant of south China, is a perennial herb and its fruit is of importance for traditional medicine and spice in many Asian countries. For economic purpose, *A. villosum* was introduced into tropical seasonal rainforests of Xishuangbanna from Guangdong province, southeast China in 1963. Now *A. villosum* has become an important component of understory in humid subtropical and tropical forests with almost 58.11 km^2 of cultivated area and developed an important economical source for local minority people (Liu *et al.* 2006). *Amomum villosum*, as a clonal plant, can grow in the understory with 5–85% irradiance (Zhou 1993, Yang *et al.* 1995) through stolons. They tended to grow and stretch their spreading stems along tropical ravine rainforest. It can grow and attain a high yield even in environments with direct sunlight for several hours each day (Feng *et al.* 2002a). In different light environments, they show obviously different morphological and ecophysiological characteristics (Feng and Li 2007). Photosynthesis or photoinhibition of *A. villosum* in natural environments has been studied extensively (Feng *et al.* 2002a,b). In its rainforest habitat, it is hard to distinguish the different morphological plasticity and photosynthetic characteristics of *A. villosum* in different light environments due to complicated ecological environment (light, water, temperature, slope height, *etc.*). Farmers often thin out some 30% of canopy trees when they grow this plant for commercial purposes in the primary or secondary forests, which leads consequently to reduction of biodiversity in these forests. What is more, it is also observed that, once hit by bright sunlight, even under wet conditions, its leaves soon roll up to diminish light absorption (Feng *et al.* 2002a). *Amomum villosum* may also exhibit high plasticity and strong adaptability to contrasting light environments to facilitate their dominance in habitats with distinct light conditions. It is unknown whether *A. villosum* solely depends on clonal growth for ecological success or if it also employs phenotypic plasticity in different light environments. Few studies have been carried out on effects of different light environments on clonal growth of *A. villosum*.

The objective of this study was to examine how the clonal growth and photosynthesis of *A. villosum* respond to different light environments and to provide support for *A. villosum* cultivation in rainforest. Clonal growth, morphological characteristics, photosynthesis parameters, chlorophyll (Chl) fluorescence and contents were determined in *A. villosum* plants after their exposure to different light environments.

Materials and methods

Plant material and experimental conditions: The experiment was conducted in experimental fields in Yunnan Branch Institute of Medicinal Plant Development, Chinese Academy of Medical Sciences (21°27'N, 100°25'E), which is situated in the southern part of the Yunnan Province, south-west China. Mean annual temperature is 20–22°C and annual precipitation is 1,947 mm. With a strong seasonality, more than 85% of precipitation occurs during the wet season (July–November). The new ramets of *A. villosum* with one or two fresh leaves were transplanted in November, 2014 from understory of forest to the experimental fields. Artificial shade was obtained through the use of different shading nylon nets, fixed in bamboo frames with dimensions of 3 × 2 × 1.5 m under field conditions; it created three irradiance levels of about 15% [about 300 μmol(photon) m^{-2} s^{-1}, S15], 30% [about

550 μmol(photon) m^{-2} s^{-1}, S30], and 60% [about 1,000 μmol(photon) m^{-2} s^{-1}, S60] of global radiation [about 1,800 μmol(photon) m^{-2} s^{-1}], which was a control treatment under full sunlight (100%, FL). The forest soil was used to provide a substrate with a natural composition of macro- and micronutrients and irrigation was provided daily. All measurements were performed in April, 2015, prior to the beginning of the wet season.

Measurement of clonal growth: The growth of *A. villosum* was photographed after one and a half year (8 January, 2014–6 July, 2015) of exposure to different light environments. Five plants per treatment were harvested on 9 July, 2015 to determine their plant height, stem length, leaf length and width, a number of leaves, leaf angle, number of ramets, and stolon length. In addition, another ten leaves from each site were measured for the length and width of the leaf blade. The leaf length was measured from a base of petiole to a leaf tip, while the leaf width was measured as the maximum width of the blade. The leaf angle was measured between a petiole and stem. At the end of the experiment (a week later), all plant parts (stems, leaves, and stolons) in ramets were harvested separately and dried to constant mass at 70°C and then weighed in order to determine biomass.

Gas exchange and PPFD-response curves: Leaf photosynthesis *vs*. light-response curves were detected using a portable photosynthesis system *LI-6400* (*LI-COR Biosciences Inc*., Lincoln, NE, USA). A red-blue LED light source attached to the system was used to produce steady PPFD. All light-response measurements were made between 08:30 and 11:30 h, when photosynthesis was most likely to be at its peak. Leaves were illuminated at a PPFD of 1,000 μmol m^{-2} s^{-1} until a steady state of net CO_2 fixation was reached. The PPFD was then increased to 1,500 μmol m^{-2} s^{-1} and then decreased in a stepwise manner [1,500, 1,200, 1,000; 800, 500, 200, 100, 80, 50, 20, and 0 μmol(photon) m^{-2} s^{-1}]. The net photosynthetic rate (P_N) was recorded after exposing the leaf to each light gradient for 3–5 min until a steady state of photosynthesis was approached. During the measurements, temperature, vapor pressure, and CO_2 concentrations in the leaf chamber were maintained at 25°C, 1.5 kPa, and 380 μmol(CO_2) mol^{-1}, respectively. Light-response curves were fitted by the nonrectangular hyperbolic model (Thornley 1976). The light-saturated net photosynthetic rate (P_{Nmax}), apparent quantum yield (α), dark respiratory rate (R_D), light-compensation point (LCP), and light-saturation point (LSP) were calculated from leaf photosynthesis *vs*. light-response data.

Chl fluorescence emission was measured simultaneously on the same leaves (n = 5) used for the gas-exchange measurements, with a leaf chamber fluorometer *LI 6400-40*, a LED-based fluorescence accessory for the portable photosynthesis system *LI-6400* (*LI-COR Bioscience Inc*., Lincoln, NE, USA). In order to assess the emission of Chl fluorescence in dark-adapted leaves, the leaf tissue was placed in standard *Hansatech* leaf clips for 30 min for solar radiation reflection, decrease leaf temperature, and oxidation of the whole photosynthetic electron transport system. Following the dark adaptation, the leaf tissue was illuminated with a weak-modulated measuring beam [0.25 kHz, < 0.1 μmol(photon) m^{-2} s^{-1}, 630 nm, 1 s] in order to obtain the minimal fluorescence (F_0). A saturating white-light pulse [20 kHz; 6,000 μmol(photon) m^{-2} s^{-1}, 630 nm, 1 s] was applied to ensure maximum fluorescence emission (F_m). The maximum photochemical efficiency of PSII (F_v/F_m) was calculated by the equipment as [F_v/F_m = ($F_m - F_0$)/F_m)] (Roháček 2002, Baker 2008).

Photosynthetic pigment contents were determined in acetone extracts of leaf discs (collected from the same leaves used for the gas-exchange measurements) following Arnon (1949) and Pires (2011). The extraction of chloroplast pigments was carried out after the incubation of five leaf discs (0.5 cm^2) with 10 mL of 80% (v/v) acetone at 4°C in the dark overnight, followed by maceration until it was completely extracted. The absorbance of extracts was read in a microplate spectrophotometer (*VersaMax*, *Molecular Devices Inc.*, Sunnyvale, CA, USA) at 645, 663, and 470 nm and the Chl contents were calculated using the equations proposed by Arnon (1949).

Statistical analysis: The differences in clonal growth, leaf morphological traits, biomass, photosynthetic characteristics, and pigment concentrations in ramets under different light environments were tested using one-way analysis of variance (*ANOVA*) in *SPSS 16.0* (*SPSS Inc.*,Chicago, IL, USA), followed by the *Tukey*'s mean comparison test (p<0.05).

Results

Clonal growth: There was a large variation of clonal growth in *A. villosum* under different light environments (Fig. 1). The explained variation by the *ANOVA* model was very high and most factors showed high significance. *A. villosum* showed the higher height under shade compared to that under FL (Fig. 1*A*). *Amomum villosum* were the highest and with much more ramets under S30 and S60 than those under FL (100%) and S15 light environments (Fig. 1*B*). *Amomum villosum* attained less ramets under S15, only 8 ramets after 1.5 years of growth. Thicker stolon facilitated flowering later. The lengths of most stolons significantly responded to the light treatments. Stolons were 3–4 times longer under S30 and S60 than those under either low (S15) or high light

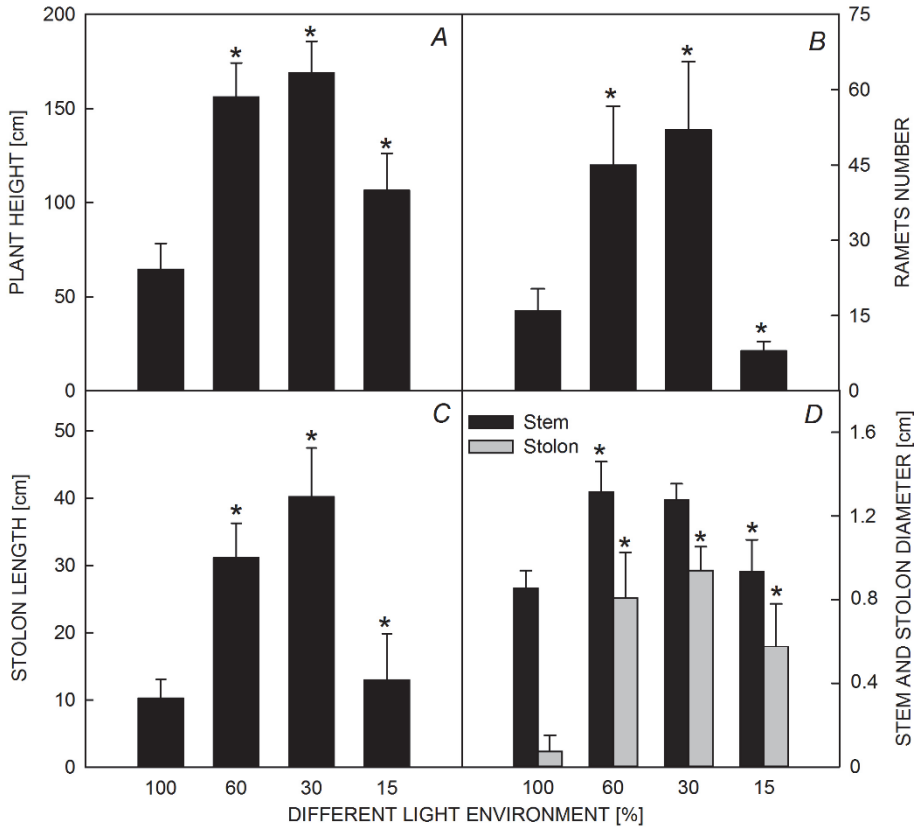

Fig. 1. Plant height (*A*), ramet number (*B*), stolon length (*C*), and stem and stolon diameters (*D*) of *Amomum villosum* in different light environments. Bars represent means ± SE from five ramet replicates and means comparison was done using *Tukey*'s test. Significant differences (p<0.05) are indicated with asterisk.

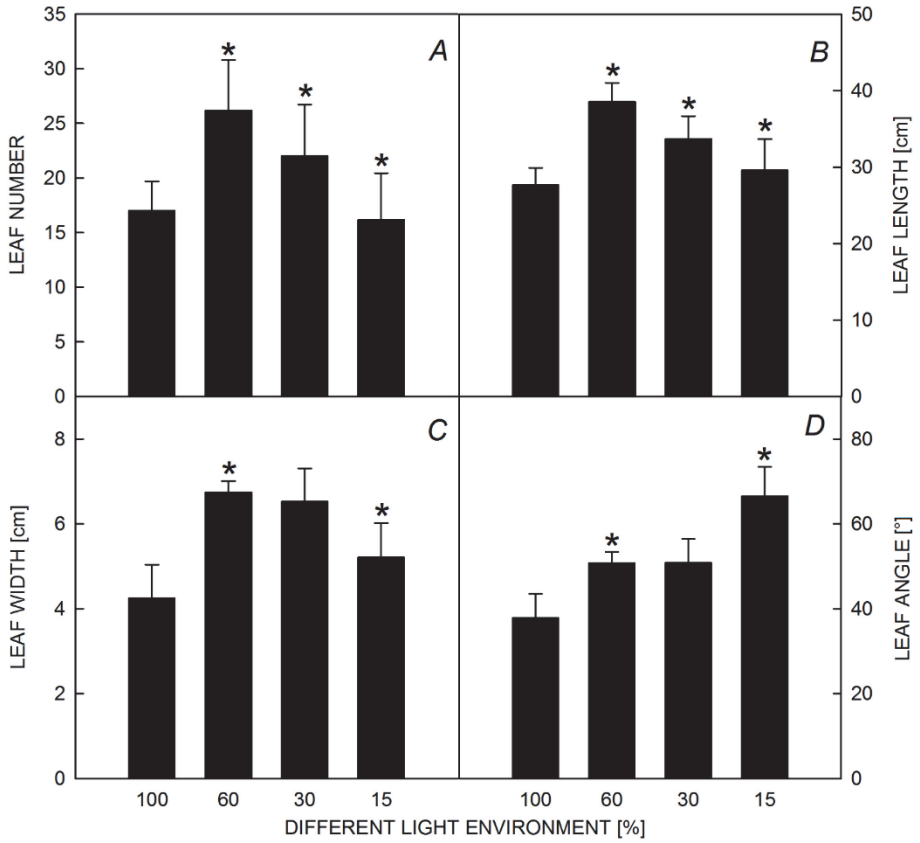

Fig. 2. Leaf number (*A*), leaf length (*B*), leaf width (*C*), and leaf angle (*D*) of *Amomum villosum* in different light environments. Bars represent means ± SE from five ramet replicates and means comparison was done using *Tukey*'s test. Significant differences (p<0.05) are indicated with asterisk.

(FL, 100%) (Fig. 1*C*). Longer stolons and more ramets made a larger population density and vigorous clonal growth of *A. villosum* under the S30 and S60 environments. The stem and stolon showed the same tendency under different light environments. Shade significantly increased the diameter of stolons on which flower buds occur (Fig. 1*D*). In general, *A. villosum* attained better clonal growth under S30 and S60, with the higher plant height, number of ramets, stolon length and diameter. The population of *A. villosum* in S15 light environment was very sparse.

Leaf morphological characteristics: There was a large variation in leaf morphology characteristics of *A. villosum* in different light environments (Fig. 2). The variation by the *ANOVA* model was very high and most factors were highly significant. *Amomum villosum* attained the highest leaf number, width, and length in S60 (Fig. 2*A,B,C*). Compared with FL (100%) environment, the shade-grown *A. villosum* possessed a larger crown area than the sun plants, but for those grown in S15. *A. villosum* allocated more biomass to upper growth (straight stem and leaves) than stolons under S60. The leaf angle significantly increased with the decreasing irradiance. The leaf angle of *A. villosum* in S15 was almost double than that under FL (Fig. 2*D*). However, this difference was not significant between S30 and S60. In the FL environment, the smallest leaf angles were observed (Fig. 2*D*).

For *A. villosum*, the artificially different light environments influenced significantly the biomass production. In different light environments, fresh and dry biomass of *A. villosum* ramets showed a trend of S30 > S60 > S15 > FL = 100% (Fig. 3). Total plant fresh or dry mass was higher in S30 and S60. *A. villosum* ramets exhibited the lowest biomass in the FL environment. The biomass of ramets in S30 and S60 was 4–6 times higher than that in FL and S15.

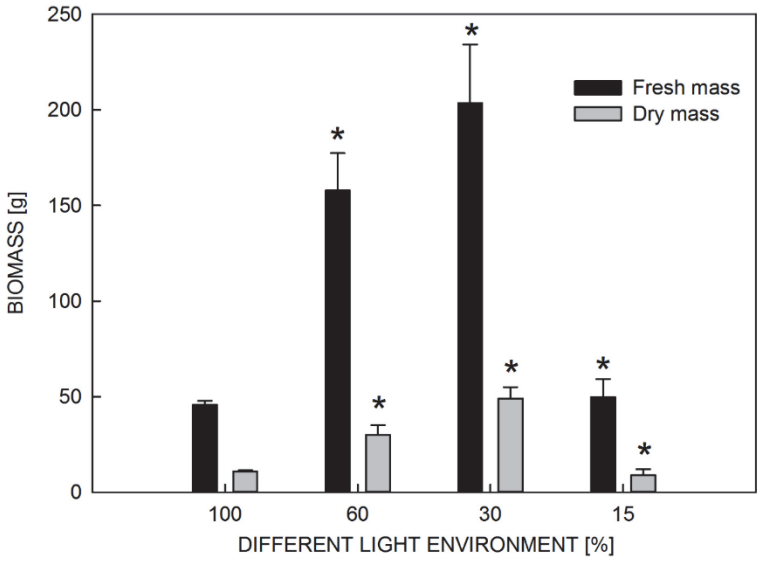

Fig. 3. Fresh and dry biomass of *Amomum villosum* ramets in different light environments. Bars represent means ± SE from five ramet replicates and means comparison was done using *Tukey*'s test. Significant differences (p<0.05) are indicated with asterisk.

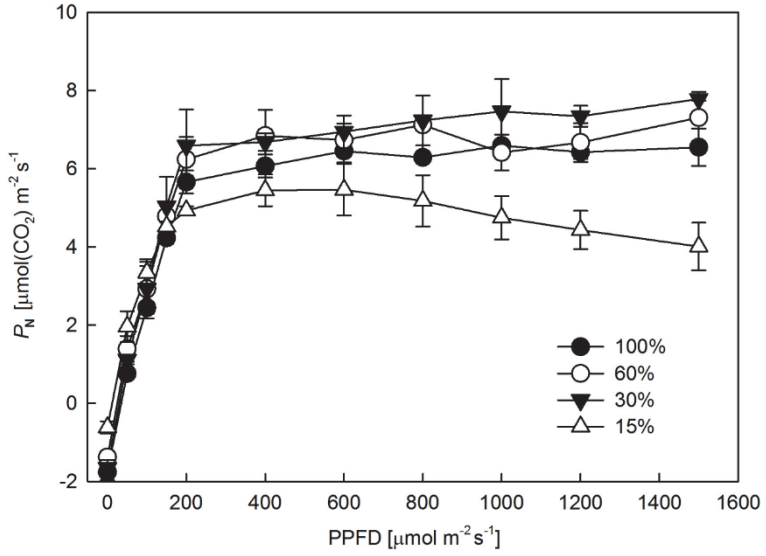

Fig. 4. Photosynthetic light-response curve of *Amomum villosum* in different light environments. These are means ± SE from five ramet replicates. Curves were fitted by a nonrectangular hyperbola model.

Table 1. Light-saturated net photosynthetic rate (P_{Nmax}), dark respiration rate (R_D), light-compensation point (LCP), light-saturation point (LSP), and apparent quantum yield (α) estimated for *Amomum vilosom* in different light environments. These are means ± SE from five replicates. Means comparison were done using *Tukey*'s test (p<0.05). For each variable *lowercase letters* indicate comparison among treatments.

Light environment	P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	α [mol mol^{-1}]	LSP [μmol m^{-2} s^{-1}]	LCP [μmol m^{-2} s^{-1}]	R_D [μmol m^{-2} s^{-1}]
100%	6.69 ± 1.37[a]	0.089 ± 0.012[a]	822.38 ± 91.9[a]	27.02 ± 3.58[a]	2.12 ± 0.13[a]
60%	7.12 ± 0.81[b]	0.096 ± 0.025[b]	836.04 ± 72.5[a]	19.09 ± 4.66[b]	1.97 ± 0.25[a]
30%	7.56 ± 0.43[b]	0.104 ± 0.011[b]	1,007.08 ± 123.6[b]	21.81 ± 6.21[c]	1.89 ± 0.19[a]
15%	5.5 ± 0.64[c]	0.084 ± 0.018[c]	493.89 ± 105.1[c]	8.79 ± 5.24[d]	0.87 ± 0.31[b]

Light-response curves and leaf gas exchange: No significant differences were observed for the parameters derived from the response curves to light between the different light levels in *A. villosum* in FL, S60, and S30 (Fig. 4). The lowest P_{Nmax}, LSP, LCP, α, and R_D values were observed under S15. For this species, the highest mean values of P_{Nmax}, and LSP were obtained in the S30 plants (Table 1). The mean P_{Nmax} of leaves in S30 was 7.56 μmol(CO_2) m^{-2} s^{-1} which was 27.2% greater than that in S15. There was no significant difference in S30 and S60 environments (Table 1). Leaves grown in S30 had the highest LSP (1,007.08 ± 123.6 μmol m^{-2} s^{-1}) and those grown in S15 had the lowest LCP (8.79 μmol m^{-2} s^{-1}). For *A. villosum*, the highest and lowest LCP values were observed at FL and S15, respectively. R_D increased with the increasing of irradiance and *A. villosum* gained the highest values in FL.

Chl fluorescence emission: The values of F_0 were significantly different in *A. villosum* in different light environments (Fig. 5*A*). The F_0 values of *A. villosum* progressively increased with the increasing irradiance. *A. villosum* gained the highest F_o values in the FL environment and the lowest values in S15. The F_v/F_m values of *A. villosum* were not significantly different between the shade levels, only being higher at S15, reducing progressively with the increase of light intensity (Fig. 5*B*).

Concentration of photosynthetic pigments: The concentrations of Chl and Car in leaves of plants under different light environments showed significant differences (Table 2). Compared with the control treatment (FL), the concentrations of Chl *a*, Chl *b*, Chl (*a*+*b*), and Car in leaves of *A. villosum* showed a tendency to increase with the decreasing irradiance. The contents in the leaves of

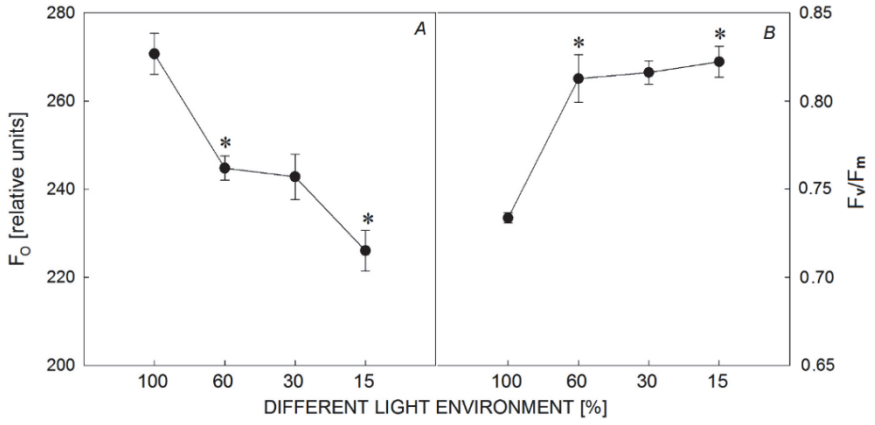

Fig. 5. Minimal fluorescence (F_0, *A*), maximum photochemical efficiency of PSII (F_v/F_m, *B*) of *Amomum villosum* in different light environments. The numbers are means ± SE from five ramet replicates and means comparison was done using *Tukey*'s test. Significant differences (p<0.05) are indicated with asterisk.

Table 2. Concentrations of chlorophyll (Chl) *a*, Chl *b*, total Chl [Chl (*a*+*b*)], Chl *a/b* ratio, and carotenoids (Car) in *Amomum villosum* in different light environments. The numbers are means ± SE from five replicates. Means comparison were done using *Tukey*'s test (p<0.05). For each variable *lowercase letters* indicate comparison among treatments.

Light environment	Chl *a* [mg g^{-1}]	Chl *b* [mg g^{-1}]	Chl (*a*+*b*) [mg g^{-1}]	Chl *a/b*	Car [mg g^{-1}]
100%	1.033 ± 0.270[a]	0.299 ± 0.075[a]	1.303 ± 0.345[a]	3.344 ± 0.058[a]	0.096 ± 0.091[a]
60%	2.089 ± 0.459[b]	0.715 ± 0.035[b]	2.804 ± 0.047[b]	2.930 ± 0.173[b]	0.974 ± 0.019[b]
30%	2.299 ± 0.229[b]	0.837 ± 0.159[b]	3.137 ± 0.385[c]	2.782 ± 0.277[c]	1.161 ± 0.173[c]
15%	2.546 ± 0.158[c]	0.977 ± 0.154[c]	3.523 ± 0.312[d]	2.632 ± 0.252[c]	1.205 ± 0.093[c]

A. villosum in FL were shown to be lower. *A. villosum* gained the highest photosynthetic pigment concentrations in S15 environment and the lowest contents in FL. The Chl *a/b* ratio showed a reversed tendency. Leaf color of the plants grown under the S15 irradiation was dark green, while those grown in FL light were yellowish green.

Discussion

In tropical rainforest, light is one of the most limiting factors affecting plant growth and survival (Poorter 1999). There was a large variation in clonal growth of *A. villosum* in different light environments. *Amomum villosum* exhibited the higher stem in the shade, resulting in the higher plants compared to the sun plants (Fig. 1). Enhanced stem elongation at low-light intensities is commonly observed in plants, and is generally interpreted as a way how to increase light harvest by moving into brighter areas (Liscum and Stowe Evans 2000). By means of a plastic response in the stem length, plants may attain a position in the regrowing canopy. *A. villosum* had longer stolons and more ramets, higher branching intensity, larger leaves, and thicker stems under S30 and S60 shade environments, similarly to previous study (Dong and Pierdominici 1995, Feng and Li 2007). Shade significantly increased the diameter of stolons on which flower buds occur. Longer stolons and more ramets made larger population density and vigorous clonal growth of *A. villosum* in the S30 and S60 environment. Shade-induced shortening of stolons in the S15 shade environment might result from very low photon flux density. More ramets showed higher branching intensities in the S30 and S60 shade environments. Our results suggest that stolons possess a unique functional role in clonal *A. villosum*. Stolons are able to store effectively meristems for future regeneration of the plants. Thicker stolons facilitate more flowering buds later. Therefore, the stolons serve mainly as storage organs of meristems and carbohydrates, and primarily as harvesting organs for light. In general, *A. villosum* attained vigorous clonal growth under the S30 and S60 shade environments, with the higher plant height, more ramets, and longer and thicker stolons.

In this study, the leaf number, length, and width was increasing with the decreasing light (Fig. 2). In this way, the photosynthetic capacity was enhanced in low-light environments. The increase in the leaf length and width was caused by changes in leaf dimensions and shape as a response to increasing shade. The leaf expansion under low irradiance is frequently reported and indicates the way how plants compensate for the decrease in light, making better use of this resource by increasing a surface area (Campos and Uchida 2002). The increased leaf surface area may improve light harvesting per unit of resources invested in construction of photosynthetic tissues (Lusk *et al.* 2008); it represents an adaptive mechanism, demonstrating the most efficient utilization of photoassimilates (DaMatta 2004, Chaves *et al.* 2008). The low leaf length and width observed in FL (Fig. 2*B*,*C*) may have benefited *A. villosum* in decreasing the exposure of plant tissues to the sun and reducing water loss and self-shade (Matos *et al.* 2009). The leaf angle decrease under high light is interpreted as a mechanism to protect the plant from excessive energy in full sunlight, while the increased leaf angle is favourable for absorbing more light in low-light environments (Schneider *et al.* 2006).

The lower values of P_{Nmax}, LSP, and higher LCP and R_D observed for *A. villosum* in FL (Table 1) indicated that the plants were stressed. Such values are a consequence of the photoinhibition, which is a slow and reversible reduction of photosynthetic efficiency under high light and which causes the partial decrease of converting the radiant energy into dry mass (Laing *et al.* 1995). Long exposure to excessive light may cause photodestruction of the photosynthetic pigments and the death of cells or organism. Generally, shade-tolerant species are more sensitive to photoinhibition than sun-adapted species (Barth *et al.* 2001). The fact that *A. villosum* survived under FL, but with the significantly lower photosynthetic rates, indicated that such species may resist to such conditions. However, cultivation at full sunlight did not seem to be the best way for the growth and development of these plants. The plants tended to have a greater capacity for photosynthetic electron transport and for ATP synthesis per unit of Chl. The highest value of P_{Nmax} in *A. villosum* under shade with increasing shade levels (except S15), showed the acclimation of this species to moderate light environments (60–30%) (Aleric and Kirkman 2005, Pires *et al.* 2011). Photosynthesis in shaded environments requires the maximization of absorbed light, together with low rates of carbon losses through respiration (Zhang *et al.* 2003); these plants present extremely reduced values of LCP, mainly due to their low values of R_D (Chen and Klinka 1997). The P_{Nmax} and LSP of this species in S30 were significantly higher than those in S15. This response followed the same pattern reported by other studies (Huang *et al.* 2011, Zhang *et al.* 2012). Plants adapted to shade environments are more photosynthetically efficient at low light levels, while they loose such efficiency under high light levels (Leverenz 1995). This indicates that lower light energy was necessary to reach P_{Nmax} and plants showed physiological plasticity which enables the adaptation to lower energy uptake (Aleric and Kirkman 2005).

F_o and F_v/F_m are good indicators of environmental stress on photosynthesis. The values of F_v/F_m varied from 0.75 to 0.85, which shows the efficient conversion of light energy at PSII (Baker 2008). *A. villosum* gained the highest F_o values under FL and the lowest values in S15. The F_v/F_m values of *A. villosum* were reduced progressively with the increase of light and *A. villosum* cultivated at full sun light gained the lowest F_v/F_m values (Fig. 5). The higher F_o values and lower F_v/F_m values indicated that *A. villosum*

was subjected to more stress under FL environment than that in the shade environment.

Plant light-acclimation strategies include mechanisms for effective light harvesting at low-light conditions as well as protection against excessive light. Changes in photosynthetic pigments are a common light-acclimation strategy among plants. Compared with those in the FL environment, the concentrations of Chl *a*, Chl *b*, Chl (*a*+*b*), and Car in leaves of *A. villosum* showed a tendency to increase with the decreasing irradiance (Table 2). The highest Chl concentration in the most shaded plants may be considered a compensation effect at the lowest light availability (Pires *et al.* 2011). The shade-adapted *A. villosum* possessed higher proportions of Chl *b*, which resulted in the decreased Chl *a/b* ratio. This contributed to *A. villosum* acclimation to shade since Chl *b* is the main component of the LHC protein (Koike *et al.* 2001, Catoni *et al.* 2015), which acts as an antenna complex in transferring light energy to the reaction center of PSII (Lam *et al.* 1984). Accordingly, shade leaves can trap more light energy through LHCII to promote a higher photosynthetic efficiency (Huang *et al.* 2011). On the contrary, leaves in sun plants have relatively low Chl *b* content (*i.e.*, higher Chl *a/b* ratio) and, in turn, a low light-trapping ability in the antennae of LHC. Through this mechanism more light energy can be dissipated as heat and fluorescence avoiding severe damage to reaction centers (Bailey *et al.* 2004). Leaf color of the plants grown under S15 was dark green, while the color of those grown in FL was yellowish-green. These all indicated that in lower-light environment higher Chl contents facilitated *A. villosum* to capture more available light energy. Lower pigment concentrations indicated that stronger light intensity destroyed photosynthetic pigments in *A. villosum* in FL environment.

Conclusions: In this study, *A. villosum* exhibited a strong plasticity in clonal growth, morphological, and photosynthetic characteristics. This high plasticity in clonal growth may partially explain its ecological success and expansion in varied light environment in rainforest. Better clonal growth in 30–60% light environments with higher photosynthetic rates showed that *A. villosum* adapted to the moderate shade conditions. *Amomum villosum* probably experienced some stress in 100% sunlight environment. In 15% light environment, the irradiance was too weak to ensure better clonal growth of *A. villosum*. That was also verified by low photosynthesis and higher contents of photosynthetic pigments. This information is very useful for selection such clonal species for rainforest or understory projects, and provide support for cultivation of *A. villosum* in the rainforest, which should avoid full light or too low-light environments.

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