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CHLOROPHYLL FLUORESCENCE AND GROWTH RESPONSES OF DIFFERENT DWARF BAMBOO SPECIES TO DROUGHT STRESS

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Abstract

Physiological responses and changes in growth of dwarf bamboo under drought stress are essential for establishing an evidence-based management system to maintain soil moisture for optimal growth. In this study, the responses of chlorophyll fluorescence, moisture content, and biomass accumulation of nine dwarf bamboo species placed in a drought stress environment were investigated. The species with large leaves, such as *Indocalamus decorus* Q. H. Dai and *Sasaella glabra* (Nakai) Koidz. f. *albo-striata* Muroi, had higher initial photosynthetic efficiency indexes than species with small leaves, such as *Sasa fortunei* (Van Houtte ex Munro) Fiori and *Sasa pygmaea* (Miq.) Rehder, but their initial light protection indexes were lower. As drought stress increased, photosynthetic efficiency indexes of large-leaved bamboo species dropped more than those of small-leaved species. In contrast, light protection indexes of large-leaved bamboo species dropped less than those of small-leaved species. The average stem and rhizome moisture content of all the bamboo species decreased tardily. However, the average moisture content of the leaf and root decreased abruptly. The initial biomass accumulation ratios of the large-leaved bamboos were higher than those of the small-leaved species. As the drought stress increased, the biomass accumulation ratio of large-leaved bamboo species declined rapidly, even falling below that of the small-leaved species, which did not decline as much. In conclusion, the biomass productivity of small-leafed dwarf bamboo species was found to be higher than that of large-leaved species under prolonged drought stress.

Key words: Dwarf bamboo; Drought stress; Chlorophyll fluorescence; Moisture content; Biomass accumulation; Comprehensive evaluation.

Introduction

Drought is usually defined as a joint interaction between rainfall reduction, groundwater level decline, and limited water availability due to increased temperature (Singh *et al.*, 2015; Singh & Laxmi, 2015), and it is one of the most important stress factors affecting the normal growth and development of plants (Joshi *et al.*, 2016). Water shortages have become a serious problem that restricts the development of agriculture and forestry, so plant responses to and adaptation mechanisms for drought stress have been the focus of much research. In many regions of the world, there have been considerable changes in the nature of droughts and extreme temperature events since the middle of the twentieth century (Lesk *et al.*, 2016). In recent years, extreme high temperatures have negatively affected forestry in South China and have posed a serious threat to the growth of bamboo (Xu *et al.*, 2016), which is widely distributed in southern China. Dwarf bamboos are valued for their beautiful appearance and clonal reproduction, and are excellent ornamentals. They have a well-developed rhizome system that can facilitate soil and water conservation, can be widely used in landscaping and ecological restoration of abandoned mines, construction wasteland, and rocky decertified sites, and they have the potential to replace other grasses in lawns in the future. As the incidence of high temperatures and drought events is likely to increase, the application and popularization of dwarf bamboo is likely to suffer.

To date, the studies on drought stress in dwarf bamboo mainly fall into two categories: physiological and biochemical changes of different or the same bamboo species. Zhao *et al.* (2010) measured the plasma membrane permeability, malondialdehyde (MDA) content, free proline content, and other physiological and biochemical indexes of four dwarf ornamental bamboo species, namely *Pleioblastus kongosanensis* Makino, *Sasa fortunei* (Van Houtte ex Munro) Fiori, *Sasa argenteostriata* (Regel) E. G. Camus, and *Sasa auricoma* (Mitford) E. G. Camus, under drought stress, and evaluated their drought resistance. Liu *et al.* (2011) measured the chlorophyll content and photosynthesis of *Sasa argenteostriata*, *Pleioblastus kongosanensis*, *Sasa fortunei*, and *Shibataea chinensis* Nakai, under drought stress in autumn and analyzed their responses. Lin & Ding (2006) also studied the leaf chlorophyll content, superoxide dismutase, MDA and plasma membrane permeability of *Sasa argenteostriata*, *Pseudosasa japonica* (Siebold & Zucc. ex Steud.) Makino ex Nakai var. *tsutsumiana* Yanagita, and *Bambusa ventricosa* McClure, under drought stress and evaluated their drought resistance. These studies all lacked an evaluation of physiological and biochemical characteristics of bamboo species during different periods of drought stress and only included one comprehensive evaluation of all parameters. According to our previous studies (Gao *et al.*, 2016a; 2016b; 2016c) on lateral bud germination characteristics, photosynthesis and morphological plasticity of dwarf bamboo are very adaptable during growth in heterogeneous environments. Although trend changes of a single index with drought stress have been documented, the comprehensive drought tolerance characteristics of different bamboo species in different drought stress periods are not well known, and this information is very important for further understanding the growth regulation and adaptation mechanisms of bamboo to drought stress.

Several studies have compared drought stress responses within individual bamboo species under different conditions. Liu *et al*. (2014; 2015) used *Fargesia rufa* T. P. Yi and *Fargesia denudata* T. P. Yi, which are primarily eaten by pandas, as their research materials, and studied the response mechanisms of carbon and nitrogen metabolism under different levels of drought stress. Li *et al.* (2011) studied variation in *Pleioblastus kongosanensis* morphology, leaf water content, leaf water potential, photosynthetic parameters, and chlorophyll fluorescence parameters relative to soil water content under natural drought stress, and through experiments with potted plants. Hu *et al.* (2015) studied antioxidant enzyme activity, relative conductivity, MDA content, soluble protein content, photosynthetic pigment content, and water balance of *Indocalamus decorus* Q. H. Dai with different planting substrates and relative water contents, which provided a reference for evidence-based watering management for bamboo cultivation. This kind of research is more in-depth, but comparisons between different bamboo species are absent, and all these studies focused on biochemical and photosynthetic physiological research and did not focus on individual and population growth characteristics of bamboo under drought stress. Changes in the stem, leaf, rhizome size and biomass were not considered.

To explore the ecological adaptation mechanism of different dwarf bamboo species to drought stress, thoroughly evaluate the physiological and growth response characteristics of bamboo during different drought stress periods and attempt to establish a relatively scientific comprehensive evaluation system for bamboo growth, nine species of economically important dwarf bamboo were selected for experiments with artificially induced drought stress. The responses of chlorophyll fluorescence, moisture content, and biomass accumulation to drought stress were analyzed, as were changes in growth as drought stress was prolonged. The different responses and adaptability of the different bamboo species to drought stress will provide evidence for soil moisture management and application for these valuable species of dwarf bamboo.

Materials and Methods

Test site and materials: Bamboo plantlets were grown at the Taihuyuan ornamental bamboo garden in Ling'an City, Zhejiang Province, China (29°56′–30°23′N, 118°51′–119°72′E). The region has a warm and humid subtropical monsoon climate with four distinct seasons. The annual precipitation is 1,250–1,600 mm and the annual average temperature is 15.4°C. The monthly average temperature ranges from 3.2°C in January to 29.9°C in July, with recorded extremes of −13.3°C and 40.2°C. The ≥ 10°C annual accumulated temperature is 5,100°C, the annual frost-free period is 235 d, and the annual sunshine hours vary between 1,850 and 1,950. The soil is a fertile red loam more than 60 cm deep, with a loose structure that is very suitable for growing bamboo plants.

The characteristics of the nine selected bamboo species are presented in Table 1.

Each bamboo species was introduced to the garden in 2004 and grown with similar substrates and fertilizers. The bamboo species grew well and were not affected by pests and diseases.

Experimental design: Rhizomes of each bamboo species were dug in February 2015, and two-year-old rhizomes with many lateral buds were selected for vegetative propagation. The rhizomes were cut into small, single-rhizome sections 5–6 cm long. Five to six single-rhizome sections were planted in red loam soil emended with fertilizer in one pot 20 cm (diameter) by 15 cm (depth). By October 2015, robust new bamboo plantlets developed from one lateral bud on each rhizome section. New shoots and rhizomes grew at the base of the new plantlet, and one rhizome section generally produced 3–5 new plantlets with 1–2 new rhizome(s) in a year. Rhizome sections with similarly sized plantlets were selected and pruned to remove new rhizomes and all but three plantlets. Rhizome sections with plantlets were replanted in pots 26 cm (diameter) by 23 cm (depth); each bamboo species was established in 50 pots, with 12 plantlets per pot. All plantlets were then grown for 7–8 months to recover and were watered with approximately 0.5 L of water every five days. In July 2016, a drought stress treatment was initiated during the active growth period of the bamboo plantlets. On July 2, the potted bamboo plantlets were watered for the last time, and the soil remained moist until July 7 (Table 2). On July 7 (drought stress for 0 day), July 14 (drought stress for 7 days), July 21 (drought stress for 14 days), July 28 (drought stress for 21 days), and August 4 (drought stress for 28 days), the chlorophyll fluorescence parameters, water content, and biomass indexes of each bamboo species were measured.

Determination of chlorophyll fluorescence parameters: Nine to twelve plantlets with good growth were selected for each bamboo species. On a sunny and windless day, a PAM-2500 modulated chlorophyll fluorescence analyzer was used to determine fluorescence parameters at 9:00–11:00 in the morning. In light-adapted leaves, the following parameters were measured: leaf real-time fluorescence (F_t), minimal fluorescence (F_0'), and maximal fluorescence (F_m'). After 30 min of dark adaptation, initial fluorescence (F_0) and maximal fluorescence (F_m) were measured. Based these values, the following parameters were calculated: variable fluorescence (F_v; $F_m – F_0$), PSII maximum photochemical quantum yield (F_v/F_m), PSII effective photochemical quantum yield ($Y_{(II)}$; $(F_m' − F_t)/F_m'$), two photochemical fluorescence quenching coefficients (qP; $(F_m' − F_t)/(F_m' − F_0')$) and (qL; $qP \times F_0'/F_t$); two non-photochemical fluorescence quenching coefficient (qN; $1 − (F_m' − F_0')/(F_m – F_0)$) and (NPQ; $(F_m/F_m') − 1$)), and non-photochemical fluorescence quenching quantum yield ($Y_{(NO)}$; $1/(NPQ + 1 + qL \times (F_m/F_0 − 1))$).

Table 1. Species and characteristics of bamboo used in the study.

Species	Stem height (cm)	Basal diameter (cm)	Leaf area (cm^2)
Indocalamus decorus	30.00-90.00	0.20-0.40	40.00-50.00
Sasaella glabra (Nakai) Koidz. f. *albo-striata* Muroi	20.00-60.00	0.10-0.20	35.00-45.00
Pleioblastus kongosanensis	50.00-100.00	0.20-0.30	40.00-45.00
Sasa argenteostriata	30.00-50.00	0.20-0.30	20.00-25.00
Shibataea kumasaca (Zoll. ex Steud.) Makino	100.00-200.00	0.30-0.40	15.00-20.00
Shibataea chinensis Nakai	60.00-100.00	0.20-0.30	15.00-20.00
Sasa auricoma	20.00-80.00	0.10-0.20	10.00-20.00
Sasa fortunei	15.00-40.00	0.10-0.20	10.00-20.00
Sasa pygmaea (Miq.) Rehder	20.00-40.00	0.10-0.20	3.00-8.00

Table 2. Changes of potted soil moisture content under different drought stress periods.

Date	Soil moisture content of different bamboo species (%)								
	ID	SG	PK	SAR	SK	SC	SAU	SF	SP
July 7	23.93 ± 2.14	23.71 ± 2.88	27.21 ±2.52	30.65 ± 1.96	33.33 ±2.55	31.66 ± 5.32	33.00 ± 3.41	34.82 ± 3.98	38.09 ± 2.46
July 14	15.12 ± 2.12	16.62 ± 1.87	18.32 ±4.15	18.00 ± 6.22	19.81 ±7.15	19.12 ± 4.81	24.03 ± 1.28	26.31 ± 4.64	23.92 ± 3.75
July 21	10.67± 3.12	7.84 ± 1.58	11.15 ±4.13	14.84 ± 3.62	13.22 ±3.46	10.88 ± 4.21	11.08 ± 1.59	12.07 ± 4.24	17.50 ± 9.05
July 28	5.51 ± 1.12	5.73 ± 3.23	7.86±5.46	9.00 ± 1.28	10.07 ±1.73	6.00 ± 1.27	7.01 ± 1.41	9.86 ± 2.64	9.25 ± 1.32
August 4	4.28 ± 1.11	3.35 ± 0.45	3.57 ± 0.62	4.81 ± 1.23	7.84 ±2.44	4.11 ± 1.07	4.98 ± 3.13	4.11 ± 1.75	5.62 ± 2.43

ID, *Indocalamus decorus*; SG, *Sasaella glabra*; PK, *Pleioblastus kongosanensis*; SAR, *Sasa argenteostriata*; SK, *Shibataea kumasaca*; SC, *Shibataea chinensis*; SAU, *Sasa auricoma*; SF, *Sasa fortunei*; SP, *Sasa pygmaea*. Every mean value is presented with a standard error

Plantlet moisture content and biomass measurements: Six pots were randomly selected from each bamboo species in different drought stress periods. Bamboo material was removed from the pots, washed, and dried. Fresh stems, leaves, rhizomes, and roots were removed and weighed separately, placed in a 105°C oven for 30 min, and then dried to a constant weight at 70°C. The moisture content (%) was calculated by subtracting the dry weight from the fresh weight and dividing by the fresh weight × 100. The biomass accumulation rate (%) was calculated as follows: (biomass during n_2 - biomass during n_1)/biomass during n_1 × 100, where n_1 is the current period of drought stress and n_2 is the following period.

Data analysis methods: The averages and standard deviations of chlorophyll fluorescence parameters, moisture content, and biomass accumulation rate of bamboo plantlets were calculated in Excel (Microsoft, Redmond, WA, USA). Regression analysis, correlation analysis, and principal components analysis were conducted in SPSS 17.0 (IBM, Armonk, NY, USA). The treatments were compared using a one-way analysis of variance and Student-Newman-Keuls test. Unless otherwise stated, differences were significant at $p<0.05$.

Listed below are the specific factor score models of principal components analysis.

(1). Mathematical model of each factor score:

$$F1 = a_{11}ZX1 + a_{21}ZX2 + \dots + a_{p1}ZXp;$$
$$F2 = a_{12}ZX1 + a_{22}ZX2 + \dots + a_{p2}ZXp;$$
$$Fm = a_{1m}ZX1 + a_{2m}ZX2 + \dots + a_{pm}ZXp.$$

(2). Mathematical model of synthetic factor score:

$$F = \ddot{e}1/(\ddot{e}1 + \ddot{e}2 + \dots \ddot{e}m) \times F1 + \ddot{e}2/(\ddot{e}1 + \ddot{e}2 + \dots \ddot{e}m) \times F2 + \dots \ddot{e}m/(\ddot{e}1 + \ddot{e}2 + \dots \ddot{e}m) \times Fm.$$

F1, F2, …, Fm are each factor score number; a_{1i}, a_{2i}, … a_{pi} (i = 1, …, m) are feature vectors corresponding to the eigenvalues of P parameters; ZX1, ZX2, …, ZXp are standardized processing values of the original variable of P parameters; and ë1, ë2, …, ëm are eigenvalues corresponding to each factor score.

Results

Response of chlorophyll fluorescence physiology of bamboo species to drought stress: As the drought stress was prolonged, the chlorophyll fluorescence parameters of the nine dwarf bamboo species tended to decrease (Fig. 1a to e). The initial F_v/F_m, $Y_{(II)}$, and qP of *Indocalamus decorus*, *Sasaella glabra*, and the other large-leaved bamboo species were relatively large. The maximum values of F_v/F_m, $Y_{(II)}$, and qP of *I. decorus* were 0.78, 0.68, and 0.96, respectively, and with increased drought stress, they fell to 0.19 (−0.59), 0.13 (−0.55), and 0.35 (−0.61), respectively (Fig. 1a to c). The initial F_v/F_m, $Y_{(II)}$, and qP of *Sasa fortunei*, *S. pygmaea*, and the other small-leaved bamboo species were relatively small. The maximum values of F_v/F_m, $Y_{(II)}$, and qP of *S. pygmaea* were 0.73, 0.51, and 0.84, respectively, and with increased drought stress, they fell to 0.30 (−0.43),0.25 (−0.26), and 0.42 (−0.42), respectively (Fig. 1a to c). As the drought stress increased, the parameter change curve of F_v/F_m, $Y_{(II)}$, and qP showed a gradual contraction from large-leaved to small-leaved bamboo species (Fig. 1a to c).

In contrast, the initial qN and $Y_{(NO)}$ of *Indocalamus decorus*, *Sasaella glabra*, and the other large-leaved bamboo species were relatively small. For example, the qN and $Y_{(NO)}$ of *I. decorus* were 0.23 and 0.24, respectively, and fell to 0.12 (−0.11) and 0.07 (−0.17), respectively, with increased drought stress (Fig. 1d to e). The initial qN and $Y_{(NO)}$ of *Sasa fortunei*, *S. pygmaea*, and the other small-leaved bamboo species were relatively large. The maximum qN and $Y_{(NO)}$ of *S. pygmaea* were 0.34 and 0.33, respectively, and decreased greatly to 0.10 (−0.24) and 0.08 (−0.25), respectively, with increased drought stress (Fig. 1d to e). As the drought stress increased, the parameter change curve of qN and $Y_{(NO)}$ showed a gradual dissociation type from large-leaved to small-leaved bamboo species (Fig. 1d to e).

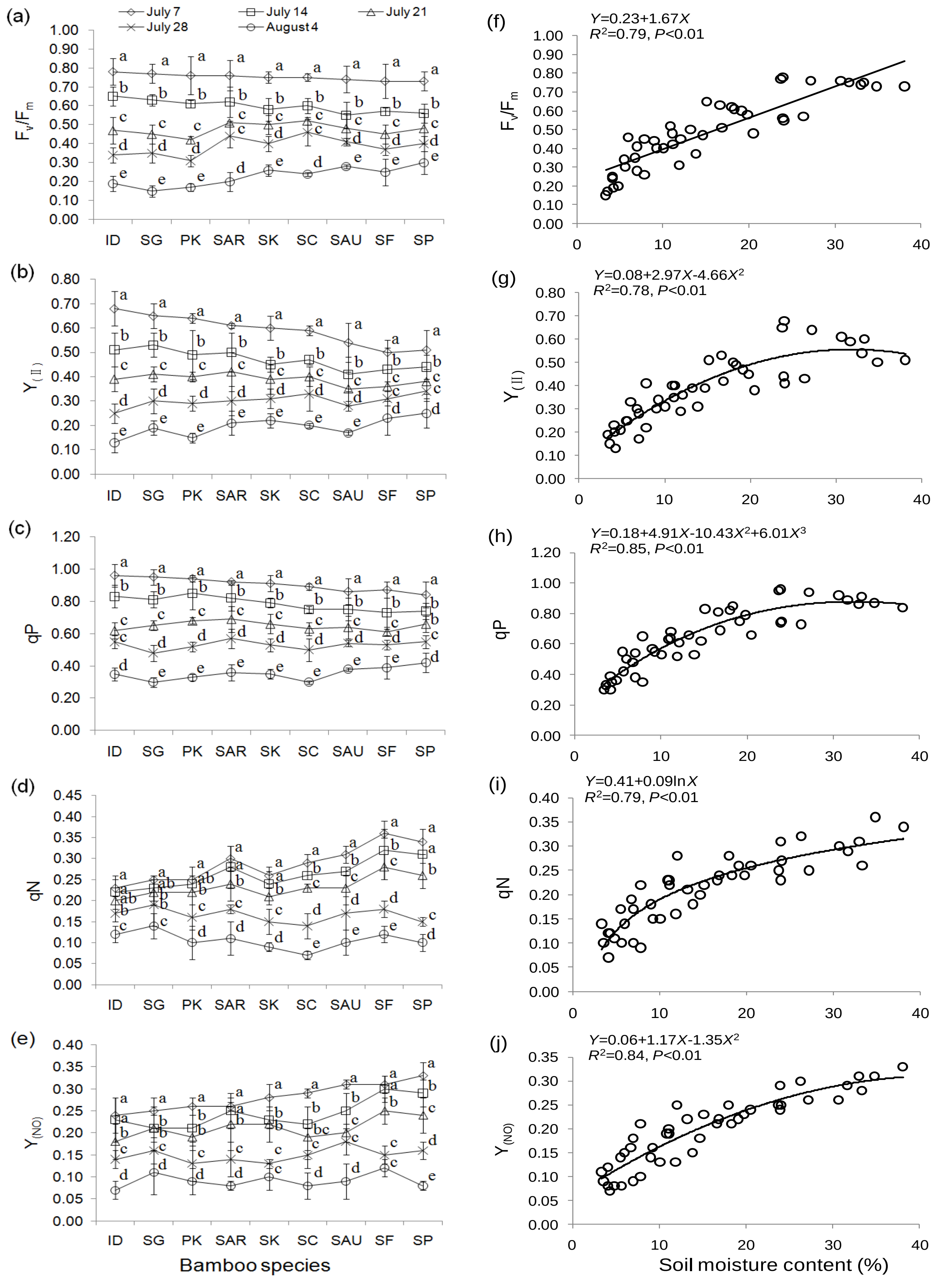

Fig. 1. Changes of chlorophyll fluorescence of different bamboo species and its relationships with soil moisture content. ID, *Indocalamus decorus*; SG, *Sasaella glabra*; PK, *Pleioblastus kongosanensis*; SAR, *Sasa argenteostriata*; SK, *Shibataea kumasaca*; SC, *Shibataea chinensis*; SAU, *Sasa auricoma*; SF, *Sasa fortunei*; SP, *Sasa pygmaea*. Vertical bars are SDs. From a to e, significance of difference gradually strengthened, its level was at 5%.

The regression equations that were fit between fluorescence parameters and soil moisture content were all extremely significant ($p<0.01$) (Fig. 1f to j). F_v/F_m and soil moisture content had a linear relationship (determination coefficient $R^2 = 0.79$) (Fig. 1f). The relationships of $Y_{(II)}$ and $Y_{(NO)}$ to soil moisture content were fit with a quadratic equation, with an R^2 of 0.78 and 0.84, respectively (Fig. 1g, j). qP and soil moisture content were fit with a cubic equation ($R^2 = 0.85$) (Fig. 1h), while qN and soil moisture content were fit with a logarithmic equation ($R^2 = 0.79$) (Fig. 1i). The changes in soil moisture content caused by drought stress significantly affected the photosynthetic efficiency and light protection ability of bamboo leaves.

Response of moisture content of bamboo species to drought stress: With increased drought stress, the moisture content of each plant part decreased (Fig. 2a to e). The stem moisture content dropped more in *Indocalamus decorus* (−31.65%), *Sasaella glabra*, (−32.44%) and the other large-leaved species than that in *Sasa fortunei* (−20.65%), *S. pygmaea* (−22.71%), and the other small-leaved species (Fig. 2a). The leaf, rhizome, root, and total moisture content declined relatively equably (Fig. 2b to e). The average moisture content of the stem and rhizome decreased slowly, from 58.80% and 56.54% on July 7 to 30.37% and 34.85% on August 4, respectively (Fig. 2a, c). The average moisture content of the leaf and root decreased quickly, from 58.16% and 61.47% on July 7 to 13.52% and 17.49% on August 4, respectively (Fig. 2b, d). This demonstrated that stem and rhizome could retain more water than the leaf and root.

The equations that were fit between different bamboo parts and soil moisture content were all very significant ($p<0.01$) (Fig. 2f to j). Both stem and total moisture content had a logarithmic relationship with soil moisture content (R^2 of 0.79 and 0.88, respectively) (Fig. 2f, j). Leaf moisture content and soil moisture content were fit by a quadratic equation ($R^2 = 0.85$) (Fig. 2g), rhizome moisture content and soil moisture content were fit by a cubic equation ($R^2 = 0.86$) (Fig. 2h), and root moisture content and soil moisture content were fit with a power equation ($R^2 = 0.86$) (Fig. 2i). Changes in soil moisture content affected water content differently in different parts of the bamboo.

Response of biomass accumulation of bamboo species to drought stress: The starting biomass accumulation rate of *Indocalamus decorus*, *Sasaella glabra*, and the other large-leaved species was higher than that of *Sasa fortunei*, *S. pygmaea*, and the other small-leaved species (Fig. 3a to e). This showed that when drought stress began, the production capacity of large-leaved species was higher than that of small-leaved species. As drought stress gradually increased, the biomass accumulation rate of *I. decorus*, *Sasaella glabra*, and the other large-leaved species decreased rapidly and even fell below that of *Sasa fortunei*, *S. pygmaea*, and the other small-leaved bamboo species. However, the decrease in small-leaved species was not great; from July 14 to August 4, the stem, leaf, rhizome, root, and total biomass accumulation rate of *I. decorus* decreased 6.95%, 7.69%, 17.49%, 10.31%, and 11.90%, respectively, but in *S. pygmaea*, they only decreased by 2.50%, 1.22%, 2.20%, 3.69%, and 2.56%, respectively (Fig. 3a to e). This indicated that the biomass accumulation rate of large-leaved species was more sensitive to drought stress.

The rhizome biomass accumulation rate of *Shibataea kumasaca*, *Shibataea chinensis*, *Sasa auricoma*, *Sasa fortunei*, and *Sasa pygmaea*, the species with medium and small leaves, scarcely changed (Fig. 3c), indicating that it was not overly affected by drought stress. The stem and rhizome biomass accumulation rate curve of *Indocalamus decorus*, *Sasaella glabra*, and the other large-leaved bamboo species showed a gradual decrease. In *I. decorus*, the stem biomass accumulation rate decreased from 7.21% on July 14 to 4.04% on July 21, and from 0.43% on July 28 to 0.26% on August 4 (Fig. 3a). Its rhizome biomass accumulation rate decreased from 17.87% on July 14, 7.38% on July 21, and 1.57% on July 28 to 0.38% on August 4 (Fig. 3c). However, the biomass accumulation rate curves for *I. decorus* leaves and roots were much more abrupt, with a leaf biomass accumulation rate that decreased from 7.93% on July 14 to 1.68% in July 21 (Fig. 3b), and a root biomass accumulation rate that decreased from 10.71% on July 21 to 3.10% on July 28 (Fig. 3d).

The R^2 of the equations fit between the biomass accumulation rate of each plant part and the soil moisture content were low, but they were all significant ($p<0.05$) (Fig. 3h) or very significant ($p<0.01$) (Fig. 3f, g, i, j). The stem biomass accumulation rate and soil moisture content were fit with a power equation ($R^2 = 0.58$) (Fig. 3f), the leaf biomass accumulation rate and soil moisture content were fit with an exponential equation, ($R^2 = 0.52$) (Fig. 3g), and the rhizome, root, and total biomass accumulation rates with soil moisture content were fit with a sigmoidal equation (R^2 of 0.33, 0.58, and 0.57, respectively) (Fig. 3h, i, j). This indicated that the change in soil moisture content from drought stress significantly affected the biomass accumulation, which reduced biomass productivity in the bamboo species.

Correlations among chlorophyll fluorescence, moisture content, and biomass accumulation rate of bamboo species: The soil moisture content was significantly positively correlated with the chlorophyll fluorescence parameters and moisture content of bamboo ($p<0.05$), and positively but not significantly correlated with the biomass accumulation rate ($p>0.05$) (Table 3). The chlorophyll fluorescence and moisture content of bamboo were sensitive to drought stress. Chlorophyll fluorescence parameters were positively and significantly correlated with each other ($p<0.05$), except for the correlation between $Y_{(II)}$ and qN, which was not significant ($p>0.05$) (Table 3).

The chlorophyll fluorescence parameters were significantly or very significantly positively correlated with bamboo moisture content ($p<0.05$) (Table 3), indicating that changes in moisture content had a great effect on chlorophyll fluorescence physiology. The correlations between chlorophyll fluorescence parameters and the biomass accumulation rate of each plant part were not significant overall ($p>0.05$), but F_v/F_m, $Y_{(II)}$, qP, and the root biomass accumulation rate had significant or very significant positive correlations ($p<0.05$) (Table 3).

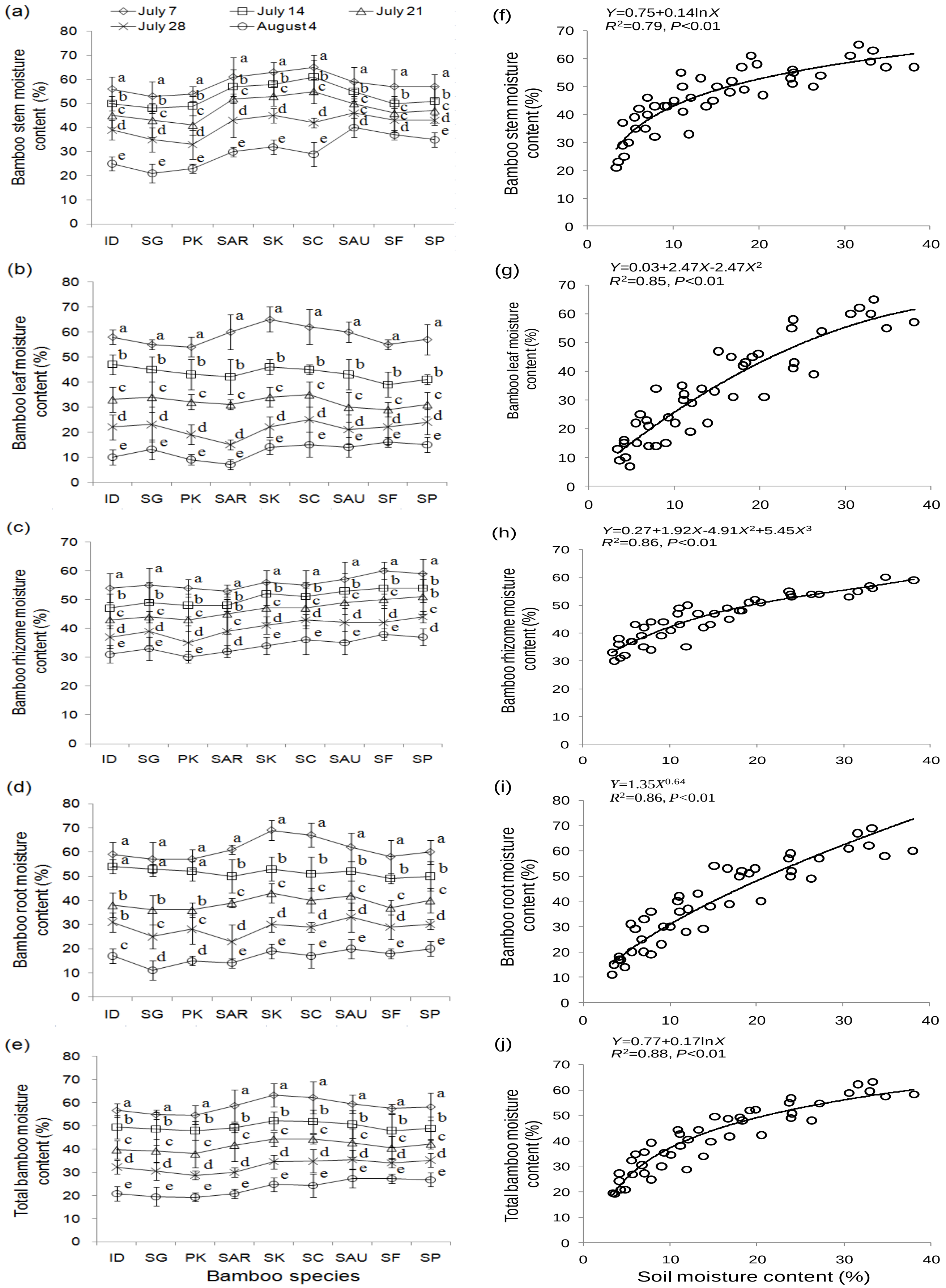

Fig. 2. Changes of moisture content of different bamboo species and its relationships with soil moisture content. ID, *Indocalamus decorus*; SG, *Sasaella glabra*; PK, *Pleioblastus kongosanensis*; SAR, *Sasa argenteostriata*; SK, *Shibataea kumasaca*; SC, *Shibataea chinensis*; SAU, *Sasa auricoma*; SF, *Sasa fortunei*; SP, *Sasa pygmaea*. Vertical bars are SDs. From a to e, significance of difference gradually strengthened, its level was at 5%.

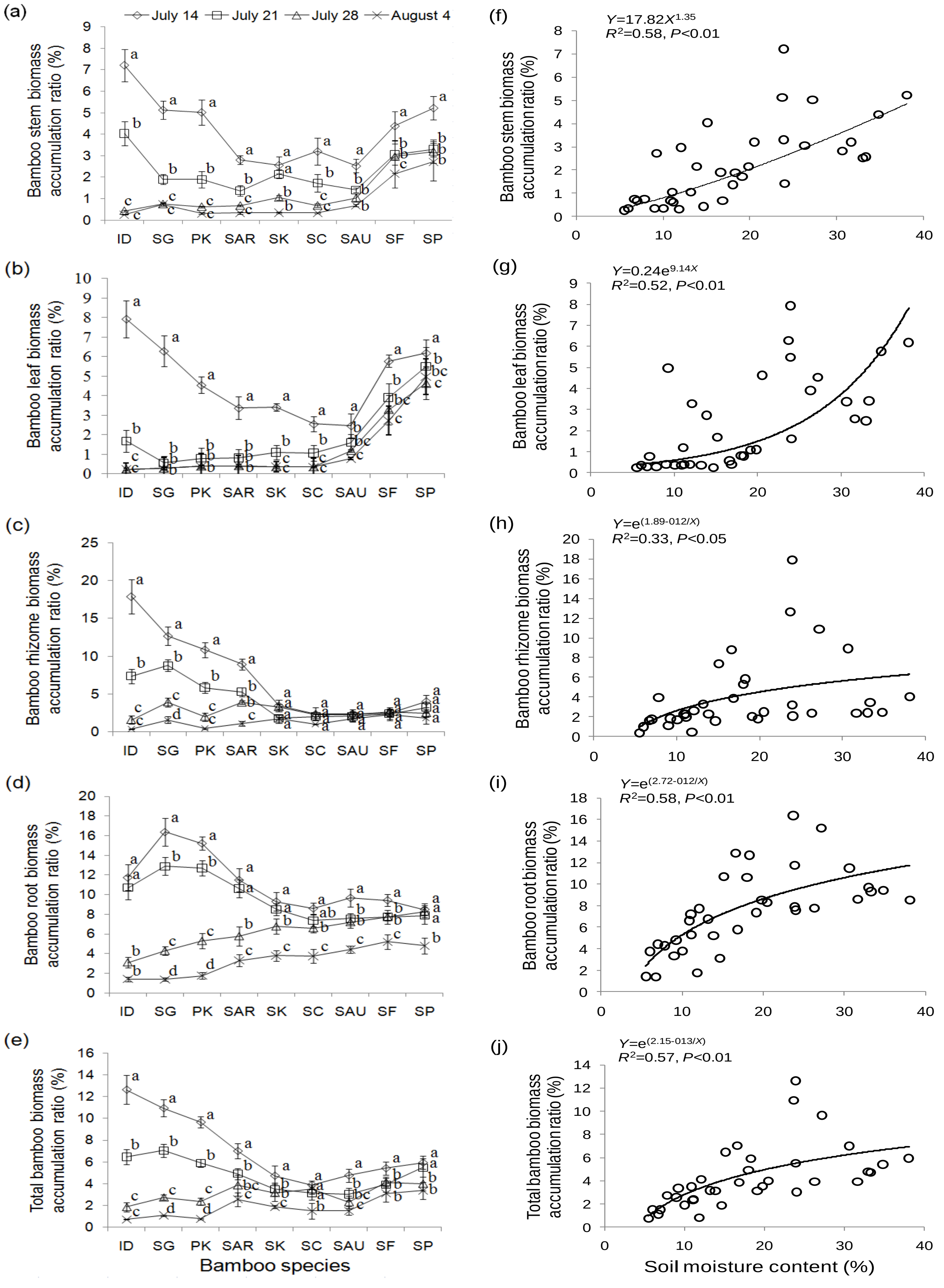

Fig. 3. Changes of biomass accumulation ratio of different bamboo species and its relationships with soil moisture content. ID, *Indocalamus decorus*; SG, *Sasaella glabra*; PK, *Pleioblastus kongosanensis*; SAR, *Sasa argenteostriata*; SK, *Shibataea kumasaca*; SC, *Shibataea chinensis*; SAU, *Sasa auricoma*; SF, *Sasa fortunei*; SP, *Sasa pygmaea*. Vertical bars are SDs. From a to d, significance of difference gradually strengthened, its level was at 5%.

Table 3. Correlation matrix (Pearson r) among chlorophyll fluorescence, moisture content and biomass accumulation ratio.

Indexes	SOMC	F_v/F_m	$Y_{(II)}$	qP	qN	$Y_{(NO)}$	STMC	LMC	RHMC	ROMC	TMC	SAR	LAR	RHAR	ROAR	TAR
SOMC	1.00															
F_v/F_m	0.89*	1.00														
$Y_{(II)}$	0.84*	0.97**	1.00													
qP	0.86*	0.98**	0.97**	1.00												
qN	0.87*	0.84*	0.79	0.86*	1.00											
$Y_{(NO)}$	0.90*	0.90*	0.85*	0.89*	0.97**	1.00										
STMC	0.82*	0.92*	0.86*	0.90*	0.82*	0.86*	1.00									
LMC	0.91*	0.97**	0.96**	0.96**	0.84*	0.90*	0.89*	1.00								
RHMC	0.90*	0.93**	0.89*	0.91*	0.92*	0.96**	0.91*	0.93**	1.00							
ROMC	0.91*	0.97**	0.94**	0.97**	0.87*	0.92*	0.92*	0.98**	0.94**	1.00						
TMC	0.91*	0.98**	0.95**	0.97**	0.88*	0.93**	0.95**	0.98**	0.96**	0.99**	1.00					
SAR	0.77	0.80	0.81	0.79	0.69	0.76	0.64	0.78	0.80	0.76	0.77	1.00				
LAR	0.72	0.67	0.66	0.65	0.63	0.68	0.53	0.65	0.73	0.62	0.64	0.93**	1.00			
RHAR	0.49	0.71	0.80	0.73	0.44	0.50	0.50	0.66	0.56	0.63	0.62	0.77	0.62	1.00		
ROAR	0.76	0.92*	0.93**	0.94**	0.78	0.82*	0.80	0.87*	0.86*	0.89*	0.88*	0.80	0.65	0.80	1.00	
TAR	0.70	0.87*	0.91*	0.88*	0.67	0.72	0.69	0.81	0.77	0.80	0.80	0.90*	0.77	0.94**	0.92*	1.00

*, ** indicate significance at 0.05, 0.01 level, respectively. SOMC, Soil moisture content; STMC, Stem moisture content; LMC, Leaf moisture content; RHMC, Rhizome moisture content; ROMC, Root moisture content; TMC, Total moisture content; SAR, Stem accumulation ratio; LAR, Leaf accumulation ratio; RHAR, Rhizome accumulation ratio; ROAR, Root accumulation ratio; TAR, Total accumulation ratio

Table 4. Component matrix and contribution rate of extracted principal components of bamboo growth under different drought stress periods.

Date	Principal component	Contribution rate (%)	Component matrix															
			SOMC	F_v/F_m	$Y_{(II)}$	qP	qN	$Y_{(NO)}$	STMC	LMC	RHMC	ROMC	TMC	SAR	LAR	RHAR	ROAR	TAR
	PC1	62.62	-0.94	0.89	0.86	0.90	-0.77	-0.88	-0.67	-0.50	-0.63	-0.59	-0.75	----	----	----	----	----
July 7	PC2	26.59	-0.25	0.44	0.50	0.38	-0.55	-0.44	0.69	0.81	-0.68	0.75	0.62	----	----	----	----	----
	PC3	6.56	0.07	0.08	0.04	-0.02	-0.08	0.04	0.14	0.25	0.20	0.22	0.22	----	----	----	----	----
	PC1	57.99	-0.95	0.91	0.91	0.91	-0.88	-0.83	-0.26	0.70	-0.93	0.73	-0.07	0.70	0.60	0.97	0.86	0.97
July 14	PC2	23.76	0.15	0.13	0.20	0.09	0.37	0.46	-0.84	-0.56	-0.04	-0.34	-0.93	-0.48	-0.56	0.03	-0.08	-0.15
	PC3	9.57	-0.03	0.02	-0.11	-0.17	-0.22	0.11	-0.19	0.43	0.16	0.47	0.32	0.50	0.55	0.18	-0.45	0.14
	PC1	42.86	0.49	0.24	-0.56	-0.17	0.86	0.84	0.31	-0.60	0.96	0.36	0.50	-0.04	-0.72	0.85	0.87	0.70
July 21	PC2	24.23	0.10	0.92	0.23	0.16	-0.33	-0.19	0.92	0.49	0.07	0.78	0.84	0.51	0.54	0.47	0.37	0.66
	PC3	14.51	0.23	0.05	0.74	0.70	0.18	0.38	-0.05	0.06	-0.21	-0.31	-0.22	0.80	0.38	0.00	-0.25	0.14
	PC4	7.17	0.78	0.05	0.07	0.42	-0.17	-0.17	-0.10	-0.15	-0.07	0.18	-0.07	0.90	0.87	0.07	0.91	0.79
	PC1	43.48	0.14	0.58	0.68	0.18	-0.33	0.49	0.76	0.43	0.96	0.37	0.83	-0.37	-0.38	0.25	0.13	0.12
	PC2	17.34	0.76	-0.24	0.13	0.40	0.46	-0.30	-0.12	-0.61	-0.21	-0.55	-0.50	0.02	-0.02	0.77	-0.05	0.49
July 28	PC3	12.72	0.21	-0.59	0.21	-0.70	0.09	0.15	-0.58	0.61	-0.02	0.06	-0.05	0.03	0.19	-0.41	-0.05	-0.17
	PC4	9.87	-0.09	-0.34	-0.65	0.27	0.60	0.56	0.14	-0.10	-0.08	0.40	0.13	0.74	0.75	0.79	0.93	0.81
	PC5	9.24	-0.33	0.37	0.18	-0.39	0.52	0.44	-0.02	-0.09	0.18	-0.61	-0.12	0.40	0.37	0.22	0.15	0.55
	PC1	57.66	0.66	0.98	0.65	0.71	-0.42	0.14	0.92	0.73	0.85	0.87	0.98	0.44	0.32	0.19	-0.18	-0.10
August 4	PC2	17.93	-0.39	-0.19	0.41	-0.10	0.56	0.87	-0.06	0.44	0.42	-0.39	0.07	0.15	0.07	0.22	0.01	-0.09
	PC3	9.77	0.12	-0.01	-0.05	0.65	0.65	0.04	0.21	-0.37	-0.19	0.04	-0.01	-0.10	-0.23	0.29	-0.08	0.04

SOMC, Soil moisture content; STMC, Stem moisture content; LMC, Leaf moisture content; RHMC, Rhizome moisture content; ROMC, Root moisture content; TMC, Total moisture content; SAR, Stem accumulation ratio; LAR, Leaf accumulation ratio; RHAR, Rhizome accumulation ratio; ROAR, Root accumulation ratio; TAR, Total accumulation ratio

There were significant or very significant positive correlations among bamboo moisture content indexes ($p<0.05$) (Table 3). Moisture content indexes were significantly positively correlated with the root biomass accumulation rate overall ($p<0.05$), but they had no significant correlation with other biomass accumulation rate indexes ($p>0.05$), indicating that moisture content was an important factor for root biomass accumulation. The biomass accumulation rates of stems and leaves were significantly positively correlated with each other (correlation coefficient R = 0.93, $p<0.01$), but correlations among the biomass accumulation rates of other plant parts were not significant ($p>0.05$). There were significant or very significant positive correlations ($p<0.05$) between the biomass accumulation rate of each plant part and the total biomass accumulation rate, except for the leaf biomass accumulation rate (R = 0.77, $p>0.05$).

Comprehensive evaluation of bamboo growth under drought stress: At the first measurement date (July 7), the bamboo chlorophyll fluorescence, moisture content, and biomass accumulation rate parameters could be explained by three principal components (Table 4), with the first principal component (PC1) explaining 62.62% of the variation; the soil moisture content and chlorophyll fluorescence parameters had higher component coefficients than other parameters. After seven days of drought stress (July 14), all parameters could be explained by three principal components (Table 4), with PC1 accounting for 57.99% of the variation. In this period, soil moisture content, chlorophyll fluorescence parameters, rhizome moisture content, and rhizome biomass accumulation rate had higher component coefficients, showing that as drought stress increased, the moisture content and biomass accumulation rate of the rhizome also became more important. After 14 days of drought stress (July 21), all parameters were combined into four principal components (Table 4), and PC1 accounted for 42.86% of the variation. qN, $Y_{(NO)}$, moisture content, and the rhizome biomass accumulation rate had higher component coefficients, reflecting the changes of physiological growth of bamboo. After 21 days of drought stress (July 28), all parameters were reduced into five principal components (Table 4), with PC1 explaining 43.48% of the variation. The component coefficient of rhizome moisture content was 0.96, making it the most important factor for reflecting the bamboo growth. After 28 days of drought stress (August 4), the parameters were combined into three principal components (Table 4); PC1 explained 57.66% of the variation, and the bamboo moisture content factors were the most important.

The synthetic factor score (F) and the rank results (Table 5) of bamboo growth, at the beginning of drought stress (before July 14), indicated that the photosynthetic efficiency and biomass accumulation of *Indocalamus decorus*, *Sasaella glabra*, and the other large-leaved bamboo species were higher than those of *Sasa fortunei*, *S. pygmaea*, and the other small-leaved species. After 14 days of drought stress (including July 21, July 28, and August 4) (Table 5), the rank of *I. decorus*, *Sasaella glabra*, and the other large-leaved species dropped, while *Sasa fortunei*, *S. pygmaea*, and the other small-leaved species were ranked at the top. The average value of all parameters measured during drought stress was calculated to produce an average synthetic factor score (Table 5); the average synthetic factor score of *Sasa fortunei*, *S. pygmaea*, and the other small-leaved species was very high and highly ranked, but the average synthetic factor score of *I. decorus*, *Sasaella glabra*, and the other large-leaved species was negative and ranked lower. It indicated that under prolonged drought, the photosynthetic efficiency and biomass accumulation of small-leaved bamboo species was higher than that of large-leaved species overall.

Discussion

The physiological and growth responses of nine dwarf bamboo species were evaluated under drought conditions. The leaf chlorophyll fluorescence, bamboo moisture content and biomass accumulation were reduced in the nine dwarf bamboo species as soil moisture content decreased, as reported in other studies that found that drought stress affected photosynthetic performance and moisture content, leading to fitness and biomass decreases (Tavakol & Pakniyat, 2007; Siddiqui, 2013; Bresson *et al.*, 2015; Mathobo *et al.*, 2017). In the present study, F_v/F_m, $Y_{(II)}$, and qP were important indicators that reflected the photosynthetic efficiency of leaves (Xu, 2002; Wu *et al.*, 2005), and they demonstrated that early in drought stress, the photosynthetic efficiency of bamboo with large leaves was higher than that of those with small leaves, and with increased drought stress, the photosynthetic efficiency of large-leaved species decreased rapidly to levels below those of the small-leaved species; the small-leaved species had a relatively small decline in photosynthetic efficiency from drought stress. In contrast, the parameters qN and $Y_{(NO)}$, which are important indicators of plant light protection and light damage (Kramer *et al.*, 2004), showed that early in drought stress, the light protection ability of small-leaved species was higher than that of large-leaved species; as drought stress increased, the light protection ability decreased rapidly in small-leaved species, but the response in large-leaved species was relatively small. This suggested that changes of chlorophyll fluorescence had intraspecific and interspecific spatial and temporal heterogeneity, which reflected differences in adaptability of different bamboo species to drought stress that might be caused by leaf area, leaf pigment concentration (chlorophyll a, b, and total chlorophyll), leaf water status (Ananthi, 2016; Embiale *et al.*, 2016), or different genetic background.

Changes in the environment and resources are known to change plant growth characteristics (Maherali & DeLucia, 2001; Grether, 2005), which lead to changes in the allocation of individual resources (Cheplick, 1995), which further affects the accumulation and distribution of biomass (Bonser & Aarssen, 2003). In this study, significant positive correlations between chlorophyll fluorescence, root biomass accumulation, and bamboo moisture content were found, suggested that bamboo moisture content was an important factor for root biomass accumulation, and changes in moisture content had a great effect on chlorophyll fluorescence physiology. The change in the moisture content and root biomass accumulation rate reflected the resource redistribution in the bamboo species under drought stress, and this is consistent with the observations of Fenta *et al.* (2014) that the strong association between root parameters and whole plant productivity demonstrates the potential application of simple root phenotypic markers in screening for drought tolerance. Furthermore, it was observed that F_v/F_m, $Y_{(II)}$, and qP, which were indicators of photosynthetic efficiency, and the root biomass accumulation rate had significant or very significant positive correlations. This revealed that under drought stress conditions, the root biomass accumulation of bamboo was beneficial for water absorption, which supports the plant resources optimal allocation hypothesis (Bloom *et al.*, 1985; McConnaughay & Coleman, 1999; Poorter *et al.*, 2012).

It has been suggested that the sensitivity, tolerance, and response timing of plants to drought varies among species (Siddiqui *et al.*, 2016). For example, slow-growing species may be more sensitive than fast-growing species (Munns, 2002; Waseem *et al.*, 2006). Some drought-tolerant plants increased their fitness by reducing leaf area and stomatal conductance to transpiration (Nativ *et al.*, 1999; Ares *et al.*, 2000). At the beginning of drought stress, the large-leaved bamboo species were high in photosynthetic efficiency, plant moisture content and biomass accumulation, while under prolonged drought, the photosynthetic efficiency, plant moisture content and biomass accumulation of small-leaved bamboo species were higher than that of large-leaved species overall. Hence, it can be suggested that the large-leaved bamboo species are more sensitive to drought stress. Growth performance is essential for plant adaptation to drought (Richter *et al.*, 2012; Ma *et al.*, 2016). Plant species with higher drought tolerance exhibit less growth inhibition and have relatively higher growth and biomass production than drought-sensitive species (Türkan *et al.*, 2005; Couso & Fernandez, 2012). Therefore, small-leaved bamboo species probably have better drought tolerance and ability to regulate intracellular water relations through biomass accumulation than large-leaved species under drought stress conditions.

Table 5. Syntheticfactor score (F) and rank result of bamboo growth under different drought stress periods.

Bamboo species	July 7		July 14		July 21		July 28		August 4		Average	
	F	Rank	F	Rank	F	Rank	F	Rank	F	Rank	F	Rank
ID	3.33	1	2.83	1	-1.84	8	-1.65	8	-1.71	8	-1.16	7
SG	2.49	2	2.65	2	-1.46	7	-0.45	7	-1.67	7	-1.88	8
PK	1.82	3	1.85	3	-1.90	9	-1.69	9	-2.19	9	-2.04	9
SAR	0.50	4	0.45	4	0.94	2	-0.37	6	-1.09	6	-0.88	6
SK	-0.58	5	-0.79	5	0.81	4	-0.03	4	1.01	4	0.43	5
SC	-0.97	6	-1.22	6	0.37	5	-0.16	5	-0.09	5	0.48	4
SAU	-1.82	7	-2.89	9	0.19	6	0.54	3	1.51	3	1.10	3
SF	-2.35	8	-2.15	8	0.90	3	1.75	2	2.11	2	1.86	2
SP	-2.44	9	-1.54	7	1.99	1	2.07	1	2.13	1	2.11	1

ID, *Indocalamus decorus*; SG, *Sasaella glabra*; PK, *Pleioblastus kongosanensis*; SAR, *Sasa argenteostriata*; SK, *Shibataea kumasaca*; SC, *Shibataea chinensis*; SAU, *Sasa auricoma*; SF, *Sasa fortunei*; SP, *Sasa pygmaea*

Conclusions

In initial stage of drought stress, the photosynthetic efficiency of large-leaved dwarf bamboo species was higher than that of small-leaved species, but the light protection ability was higher in the small-leaved species; the moisture content of different parts of bamboo varied between 50.00% and 60.00%; the biomass accumulation ratio of large-leaved bamboo species was higher than that of small-leaved species. With the continued drought stress, the photosynthetic efficiency and light protection ability of the nine species of dwarf bamboo gradually decreased, and moisture content and biomass accumulation rate decreased steadily. The photosynthetic efficiency indexes of large-leaved species decreased greatly, as did the light protection ability indexes of small-leaved species. Stems and rhizomes dehydrated slowly, while leaves and roots dehydrated quickly. The biomass accumulation rate of large-leaved species decreased much more than that of small-leaved species. After prolonged drought stress, the overall growth of small-leaved dwarf bamboo species was higher than that of large-leaved species, suggesting that leaf size can be used as an indication of drought tolerance when selecting species of dwarf bamboo.

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