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Influence of drought stress on the photosynthetic characteristics and dry matter accumulation of hybrid millet

H.B. LU[*], Y.M. QIAO[*], X.C. GONG[*,+], H.Q. LI[***], Q. ZHANG[*], Z.H. ZHAO[**], and L.L. MENG[*]

Agriculture and Forestry Technologically College, Hebei North University, Zhangjiakou 075131, China[*]
Zhangjiakou Academy of Agricultural Sciences, Zhangjiakou 075000, China[**]
Department of Mathematics and Physics, Hebei Institute of Architecture and Civil Engineering, Zhangjiakou 075024, China[***]

Abstract

In order to elucidate the drought resistance and high-yield mechanism of hybrid millet, we studied the influence of drought stress on the photosynthetic characteristics and dry matter accumulation. Our results revealed that drought stress caused lesser reduction in the net photosynthetic rate, maximal quantum yield of PSII photochemistry, excitation energy capture efficiency of PSII reaction centers and in the yield of hybrid millet compared to normal millet. When drought stress occurred in the jointing stage, the percentage decrease of P_N, F_v/F_m, F_v'/F_m', and the yield of Zhangzagu3 cultivar compared to control were 27.9%, 2.6%, 25. 5%, and 1.9%, respectively, the percentage decrease of Zhangzagu5 were 37.6%, 3.9%, 28.3%, and 16.7%, respectively, the decrease percentage of Datong29 were 60.1%, 6.4%, 4%, and 23.4%, respectively. Hybrid millet showed the similar reduction in the parameters referred above, when drought stress occurred at the heading stage, but the percentage decrease was much higher than that at the jointing stage. We concluded that hybrid millet showed higher drought resistance than normal millet.

Additional key words: chlorophyll fluorescence; gas exchange; *Setaria italica* (L.) Beauv.

Introduction

The increasing water deficit has become a main environmental factor that adversely affects growth of leaves and roots, stomatal conductance, photosynthesis, and dry matter accumulation (Zhang 2007, Bijanzadeh and Emam 2010, Wang and Shangguan 2010, Aminian *et al.* 2011). Drought stress mainly affects the photosynthetic characteristics and the physiology of crops (Brestic *et al.* 1995, Xu 2002, Maghsoudi 2008). It induced the decrease of photosynthesis and leaf chlorophyll (Chl) content (Peng *et al.* 2006). Many researches indicated that drought stress has profound effects on plant physiology in general, and on productivity and growth in particular.

Zhangzagu3 and Zhangzagu5 (hybrid millet cultivars) were bred by Zhangjiakou Academy of Agricultural Sciences (China) using the technology of photo-thermo-sensitive sterility. Both cultivars are more tolerant to drought stress (Zhao *et al.* 1995, Wang *et al.* 1998, Zhang *et al.* 2010) and may contribute to elimination of negative drought effects and hunger, which have been promoted in Africa and other semi-arid areas.

In the present study, we studied the influence of drought stress on hybrid millet at the jointing stage and heading stage by analyzing the changes in leaf gas exchange, Chl fluorescence, and the dry matter accumulation. The results could be useful for studying the drought resistance and high-yield mechanism of hybrid millet and can establish the basis for the new variety breeding of hybrid millet.

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[+]Corresponding author; e-mail: gxc2004@yeah.net

Abbreviations: Chl – chlorophyll; CR – control; DS – drought stress; E – transpiration rate; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v'/F_m' – excitation energy capture efficiency of PSII reaction centers; g_s – stomatal conductance; LA – leaf area; Nmc – normal millet cultivar; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; TLA – total leaf area; WUE – instantaneous water-use efficiency; Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Φ_{PSII} – actual photochemical efficiency of PSII.

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Materials and methods

Plants and water stress treatments: The study was conducted at Hebei North University in Shalingzi (39°30′N, 113°50′E), Zhangjiakou, Hebei, China. One normal millet (*Setaria italica* (L.) Beauv) cultivar (Datong29, Nmc), and two hybrid millet cultivars (Zhangzagu3, Zha3; and Zhangzagu5, Zha5) were used in present study. All plants were grown at an experimental farm during the normal millet growing period. The soil water field capacity was 30.12%, the content of organic matter was 0.27 g kg^{-1}, available N, P, and K were 50.32, 43.22, and 170.92 mg kg^{-1}, respectively. Before the start of our experiment, all plants were watered normally; at the jointing stage, 100 healthy and uniform plants of all different varieties were selected and marked. Different watering treatments were applied through withholding watering (drought, DS, 35 ± 5% field capacity) at the jointing stage and heading stage, respectively, while one control group was provided with optimal irrigation (control, CR, 75± 5% field capacity). After 21 d of DS, the parameters of Zha3 and Zha5 were examined. Experiments were arranged in a completely random design, with three replicates for two watering regimes.

Leaf Chl content was measured according to Liu *et al.* (2012). Five fully expanded leaves from every replicate per treatment were collected at midday for the Chl content determination. Samples (0.3 g) were extracted in ethanol-acetone (1:1, v/v) at room temperature to determine the contents of Chl *a* and Chl *b* by a spectrophotometer (*752N UV*, *Shanghai Yidian (group) company*, China) at 663 and 646 nm. Chl contents were calculated as Chl *a* [mg L^{-1}] = 12.7 A_{663} – 2.69 A_{645}; Chl *b* [mg L^{-1}] = 22.9A_{663} – 4.68A_{645} (Arnon 1949).

Leaf gas exchange: The youngest fully expanded leaves were measured by using a *LI-6400XT* portable photosynthesis measuring system (*LI-6400*, *LiCor, Inc.*, Lincoln, NE, USA) with a *6400-02B* LED source providing a PPFD of 1,200 μmol m^{-2} s^{-1}. Temperature was maintained at 28°C, relative humidity at 70%, and CO_2 concentration at 380 ± 10 mmol m^{-2} s^{-1}. Net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were obtained from three plants per treatment. Instantaneous water-use efficiency (WUE) was calculated as the ratio P_N/E.

Chl fluorescence: The fully expanded leaves were measured with an integrating fluorescence fluorometer (*LI-6400-40*, *LiCor, Inc.*, Lincoln, NE, USA). After the samples were adapted to darkness for 1 h, the minimal fluorescence yield of the dark-adapted state (F_0) was measured with weak-modulated irradiation (<0.1 μmol m^{-2} s^{-1}). A 600-ms saturating flash (>7,000 μmol m^{-2} s^{-1}) was applied to determine the maximal fluorescence yield of the dark-adapted state (F_m), variable fluorescence (F_v), and the ratio of F_v/F_m was calculated. Immediately afterwards, the leaf was continuously irradiated with red-blue actinic beams [1,400 μmol(photon) m^{-2} s^{-1}] and equilibrated for 30 min to record steady-state fluorescence yield (F_s). Following this irradiation, another saturation flash (>6,000 μmol m^{-2} s^{-1}) applied to determine maximal fluorescence yield of the light-adapted state (F_m'). After the flash, actinic irradiation was removed, far-red irradiation was given, and minimal fluorescence yield of the light-adapted state (F_0') was recorded (Liu *et al.* 2011). The fluorescence parameters were calculated as follows: effective quantum yield of PSII photochemistry (Φ_{PSII}) = (F_m' – F_s)/F_m' (Genty *et al.* 1989), photochemical quenching coefficient (q_P) = (F_m' – F_s)/(F_m' – F_0'), and the excitation energy capture efficiency of PSII reaction centers (F_v'/F_m') = (F_m' – F_0')/F_m' (Schreiber *et al.* 1994).

Growth: At the end of the experiment, the plant height and the basal diameter were recorded from five replicates of each treatment. The plant height was measured from the base of the stem, at the soil level, to the terminal bud of the main stem. The basal diameter was measured with a digital micrometer (0.001 mm) at the soil surface. To determine total biomass, plants were divided into leaf, stem, and spike portions. Total leaf area was obtained with a *CI-203* leaf area scanner (*CI-203 CID*, *Inc.* USA). The tissues were then rolled at 105°C, then oven dried at 80°C to constant mass, and total dry mass of leaves, stems, and spikes was measured. During harvesting, spikes of ten plants were collected to record their spike length, spike mass, spike diameter, spike number, 1,000-grain mass, and the yield.

Statistical analysis was performed using *SPSS-18.0* for *Windows* (*SPSS Inc.*, Chicago, IL, USA). The means of Zha3 and Zha5 were compared to Nmc using *t*-test.

Results

Gas exchange: Drought stress substantially decreased the Chl, P_N, E, and g_s of hybrid millet and normal millet. Nmc was more sensitive to DS, as manifested by the larger declines in all values (Chl: 60%, P_N: 63.2%, E: 65.6%, and g_s: 60.4%). However, hybrid millet was more tolerant to DS, their gas-exchange parameters and Chl declined less (Table 1). Hybrid millet showed the similar reduction when DS occurred at the heading stage, but the percentage decrease caused by DS at the jointing stage was much higher than that at the heading stage (Table 1). Drought stress also induced the increase in WUE of hybrid millet; the percentage increase in hybrid millet was much higher than that in Nmc (Tables 1, 2).

Table 1. The change of net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), chlorophyll (Chl), and water-use efficiency (WUE) of hybrid millet under drought stress at the jointing stage. * – mean difference is significant at the 0.05 level. Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Nmc – normal millet cultivar.

Variety	Treatment	P_N [μmol m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]	Chl [mg g^{-1}(FM)]	WUE [mol(CO_2) mol(H_2O)$^{-1}$]
Zha3	Drought	17.68	0.12	3.48	7.30	5.08
	Control	24.51	0.20	6.47	13.90	3.79
	Percentage	27.87*	40.00*	46.21*	47.48*	34.11*
Zha5	Drought	18.27	0.11	3.01	5.60	6.07
	Control	29.28	0.21	5.68	12.40	5.15
	Percentage	37.60*	47.62*	47.01*	54.84*	17.75*
Nmc	Drought	8.68	0.07	1.24	4.20	7.00
	Control	21.73	0.19	3.13	12.20	6.94
	Percentage	60.05	63.16	60.38	65.57	0.83

Table 2. The change of net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), chlorophyll (Chl), and water-use efficiency (WUE) of hybrid millet under drought stress in the heading stage. * – mean difference is significant at the 0.05 level. Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Nmc – normal millet cultivar.

Variety	Treatment	P_N [μmol m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]	Chl [mg g^{-1}(FM)]	WUE [mol(CO_2) mol(H_2O)$^{-1}$]
Zha3	Drought	18.54	0.10	1.89	6.20	9.81
	Control	28.71	0.24	3.78	12.40	7.59
	Percentage	35.42*	58.33*	50.00*	50.00*	29.15*
Zha5	Drought	17.36	0.08	2.03	6.00	8.55
	Control	28.07	0.24	4.24	14.90	6.62
	Percentage	38.15*	66.67*	52.12*	59.73*	29.17*
Nmc	Drought	7.83	0.05	1.45	3.20	5.40
	Control	21.47	0.22	3.63	12.20	5.91
	Percentage	63.53	77.27	60.06	73.77	14.62

Table 3. The change of maximal quantum yield of PSII photochemistry (F_v/F_m), excitation energy capture efficiency of PSII reaction centers (F_v'/F_m'), photochemical quenching coefficient (q_P), and actual photochemical efficiency of PSII (Φ_{PSII}) of hybrid millet under drought stress at the jointing stage. * – mean difference is significant at the 0.05 level. Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Nmc – normal millet cultivar.

Variety	Treatment	F_v/F_m	F_v'/F_m'	Φ_{PSII}	q_P
Zha3	Drought	0.76	0.41	0.33	0.66
	Control	0.78	0.55	0.46	0.84
	Percentage	2.56*	25.45*	28.26*	21.43*
Zha5	Drought	0.75	0.38	0.30	0.63
	Control	0.78	0.53	0.42	0.79
	Percentage	3.85*	28.30*	28.57*	20.25*
Nmc	Drought	0.73	0.31	0.21	0.53
	Control	0.78	0.50	0.40	0.80
	Percentage	6.41	38.00	47.5	33.75

Table 4. The change of maximal quantum yield of PSII photochemistry (F_v/F_m), excitation energy capture efficiency of PSII reaction centers (F_v'/F_m'), photochemical quenching coefficient (q_P) and actual photochemical efficiency of PSII (Φ_{PSII}) of hybrid millet under drought stress at the heading stage. * – mean difference is significant at the 0.05 level. Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Nmc – normal millet cultivar.

Variety	Treatment	F_v/F_m	F_v'/F_m'	Φ_{PSII}	q_P
Zha3	Drought	0.70	0.34	0.25	0.66
	Control	0.77	0.51	0.44	0.73
	Percentage	9.09	33.33*	43.18*	9.59*
Zha5	Drought	0.69	0.3	0.22	0.57
	Control	0.78	0.47	0.37	0.78
	Percentage	11.54	36.17*	40.54*	26.92*
Nmc	Drought	0.68	0.23	0.11	0.43
	Control	0.77	0.49	0.39	0.79
	Percentage	11.69	53.06	71.79	45.57

Chl fluorescence: Drought stress significantly decreased the F_v/F_m, F_v'/F_m', Φ_{PSII}, and q_P of both hybrid and Nmc millet. However, hybrid millet showed a lesser reduction in these parameters than Nmc (Table 3). Drought stress at the heading stage caused the similar effects to F_v/F_m, F_v'/F_m', Φ_{PSII}, and q_P, but the percentage of decrease in heading stage was much higher than that at the jointing stage (Table 4).

Table 5. The change of plant growth index of hybrid millet in different drought-stress stages. * – mean difference is significant at the 0.05 level. Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Nmc – normal millet cultivar.

Stage	Variety	Treatment	Dry matter accumulation Leaf [g]	Stem [g]	Spike [g]	Total biomass [g]	Plant height [cm]	Basal diameter [cm]	TLA [cm²]
Jointing	Zha3	Drought	8.27	21.43	33.93	63.63	148.50	3.98	1,588.88
		Control	9.47	24.03	34.80	68.30	169.77	4.02	1,688.32
		Percentage	12.67*	10.82*	2.61*	6.84*	12.53	1.00*	5.89*
	Zha5	Drought	11.70	23.33	28.23	63.26	151.97	3.98	2,023.83
		Control	13.63	29.96	29.33	72.92	175.17	4.06	2,232.12
		Percentage	14.16*	22.13*	3.75*	13.25*	13.24	1.97*	9.33
	Nmc	Drought	5.33	13.73	24.06	43.12	151.73	3.46	880.21
		Control	8.43	16.33	29.46	54.22	178.70	3.77	998.23
		Percentage	36.77	15.92	18.33	20.47	15.09	8.22	11.82
Heading	Zha3	Drought	7.90	19.53	28.33	55.76	166.67	3.88	1,288.12
		Control	9.47	24.03	34.80	68.30	169.77	4.02	1,688.32
		Percentage	16.58*	18.73*	18.59*	18.36*	1.83*	3.48*	23.70*
	Zha5	Drought	11.50	20.70	21.40	53.60	169.97	3.88	1,898.22
		Control	13.63	29.96	29.33	72.92	175.17	4.06	2,232.12
		Percentage	15.63*	30.91	27.04*	26.49*	2.97	4.43*	14.96*
	Nmc	Drought	6.27	11.23	15.26	32.76	169.33	3.34	680.00
		Control	8.43	16.33	29.46	54.22	178.70	3.77	998.23
		Percentage	25.62	31.23	48.20	39.58	5.24	11.35	31.88

Table 6. The change of spike character and yield of hybrid millet in different drought-stress stages. * – mean difference is significant at the 0.05 level. Zha3 – Zhangzagu3; Zha5 – Zhanzagu5; Nmc – normal millet cultivar.

Stage	Variety	Treatment	Spike length [cm]	Spike mass [g]	Spike diameter [cm]	Spike number	1,000-grain mass [g]	Yield [kg ha⁻¹]
Jointing	Zha3	Drought	26.11	26.25	3.22	110.20	2.71	5,857.10
		Control	28.85	28.77	3.26	114.30	2.75	5,968.35
		Percentage	9.50*	8.76*	1.23	3.59	1.45	1.86*
	Zha5	Drought	23.52	27.03	2.07	108.00	2.52	4,974.00
		Control	25.37	29.74	2.26	114.30	2.54	5,768.35
		Percentage	7.29*	9.11*	8.41	5.51*	0.59*	16.66*
	Nmc	Drought	21.07	19.01	2.58	99.10	2.13	2178.75
		Control	24.73	23.72	2.80	102.00	2.18	2,845.65
		Percentage	14.80	19.86	7.86	2.84	2.07	23.44
Heading	Zha3	Drought	24.48	20.55	3.11	109.60	2.59	4,900.65
		Control	28.85	28.77	3.26	114.30	2.75	5,968.35
		Percentage	15.15*	28.57	4.60*	4.11	6.00	17.89*
	Zha5	Drought	21.15	20.03	2.66	104.00	2.45	4,849.50
		Control	25.37	29.74	2.76	114.30	2.54	5,768.35
		Percentage	16.63*	32.65	3.62*	9.01*	3.35*	18.75*
	Nmc	Drought	16.16	11.10	2.55	97.60	2.04	1,920.00
		Control	24.73	23.72	2.80	102.00	2.18	2,845.65
		Percentage	34.65	53.20	8.93	4.31	6.21	32.53

Growth: Drought stress decreased the plant height, basal diameter, total biomass, LA, spike length, spike mass, spike diameter, spike number, 1,000-grain mass, and the yield of hybrid millet and Nmc (Tables 5, 6). However, the percentage decrease of Nmc was higher than those in hybrids. Furthermore, the yield of Zha3 only declined by 1.7% in contrast to the jointing stage. The similar effect of DS was observed at the heading stage, but the percentage of the change at the heading stage was higher than that at the jointing stage. It indicated that hybrid millet was more tolerant to DS and was much more sensitive to DS at the heading stage than at the jointing stage.

Discussion

Plant physiological processes, such as photosynthesis and transpiration, depend on the rapidity, severity, and duration of the drought event (Xu and Zhou 2008, Zhang *et al*. 2012). Normally, the first symptom of drought stress becomes evident at stomatal level. Stomata reduce their degree of opening to prevent desiccation (Ramanjulu *et al*. 1998, Flexas and Medrano 2002, Liu *et al*. 2004, Horiuchi *et al*. 2011, Li *et al*. 2011, Yan *et al*. 2012). Subsequently, photosynthesis is affected by internal water deficiency following stomatal closure. As a result, net photosynthesis is inevitably reduced due to decreased CO_2 availability at the chloroplast level (Shangguan *et al*. 2000, Long *et al*. 2006, Yan *et al.* 2006). In some plant species, drought also decreases net photosynthesis through nonstomatal factors, which reduce mesophyll photosynthesis capacity (Kicheva *et al.* 1994, Saccardy *et al*. 1996, Sadras 2004), such as a decreased carboxylation efficiency (Gulías *et al*. 2002, Romero *et al*. 2004a,b, Shi *et al*. 2007). Thus, the studying of the effect of drought stress on crops has theoretical and practical meaning. In present study, we investigated the gas exchange and Chl fluorescence in the different stages of hybrid millet development (Zhao *et al*. 1995, Wang 1998, Zhang *et al*. 2010) under drought stress condition. Our results indicated that hybrid millet showed the relatively high P_N and low E. To obtain the higher P_N, plants must maintain a certain stomatal aperture, but any increase in stomatal aperture can lead to greater stomatal water loss. Plants can also increase WUE by having high P_N and low E simultaneously, as it was found in hybrid millet (it showed simultaneously the high g_s) but not in Nmc, Datong29. Though DS induced the reduction in LA, Chl, P_N, and the biomass accumulation of hybrid millet and Nmc, the percentage decrease compared with the control of hybrid millet were lower than those of Nmc, resulting in the higher yield.

Chl fluorescence has been widely used to detect the effects of stress on functioning of the photosynthetic apparatus (Souza *et al.* 2004, Zhang *et al.* 2010). In the present study, hybrid millet and Nmc exhibited the different response to DS. Hybrid millet showed lesser decrease in Chl fluorescence parameters than Nmc under DS conditions (Table 1 and 2). Drought-induced reduction in F_v/F_m, F_v'/F_m' was observed and the extent of this effect was greater in Nmc than that in hybrid millet, and the effect was more apparent at the jointing stage than that at the heading stage. It indicated that hybrid millet was more drought-resistant than Nmc and the heading stage was more sensitive than the jointing stage.

Conclusion: Hybrid millet was more tolerant than normal millet during its vegetative growth under both well-watered and DS conditions. Normal millet showed higher drought sensitivity, with a greater reduction in gas exchange and chlorophyll fluorescence parameters, higher accumulation in biomass, and lesser increase in plant height, basal diameter, total biomass, TLA, and relative growth rate. By contrast, hybrid millet exhibited higher drought tolerance with a smaller reduction in gas exchange and chlorophyll fluorescence, higher accumulation in biomass, and greater increase in plant height, basal diameter, total biomass, TLA, and relative growth rate.

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