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Variability of nitrogen use efficiency by foxtail millet cultivars at the seedling stage

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Abstract – The objective of this work was to identify the genetic variation of foxtail millet (*Setaria italica*) cultivars, from three ecogeographic origins in China, regarding the uptake and utilization of N by the genotypes at the seedling stage, aiming at the genetic improvement of this crop. Seedlings of 79 cultivars were fertilized with a nutrient solution, on a sand substrate, and evaluated under low-N (LN, 0.2 mmol L^{-1}) and high-N (HN, 6.0 mmol L^{-1}) concentrations. A large variation was observed between cultivars, among the three ecogeographic regions, for shoot biomass, shoot N content and concentration, and N use efficiency (NUE), uptake efficiency (NupE), and utilization efficiency (NutE), especially under HN conditions. Cultivars of Northwest China showed the highest variation for shoot biomass, N content, NUE, and NupE. A strong positive correlation was observed between NUE and NupE, and NUE and NutE, but there was no correlation between NupE and NutE. NupE accounted for 77.6% of the total variation of NUE, and NutE for the rest. The uptake and utilization of N show a large variation among the foxtail millet cultivars at the seedling stage, and the variation of N uptake contributes more than that of N utilization to the variation of N use efficiency.

Index terms: *Setaria italica*, ecological cultivars, nitrogen uptake efficiency.

Variabilidade da eficiência de uso de nitrogênio por cultivares de milheto no estádio de plântulas

Resumo – O objetivo deste trabalho foi identificar a variação genética de cultivares de milheto (*Setaria italica*), de três origens ecogeográficas da China, quanto à captação e à utilização de N pelos genótipos no estádio de plântulas, com vistas ao melhoramento genético desta cultura. Plântulas de 79 cultivares de milheto foram fertilizadas com uma solução nutritiva, em substrato de areia, e avaliadas em condições de baixa (LN, 0,2 mmol L^{-1} N) e alta (HN, 6,0 mmol L^{-1} N) concentração de N. Observou-se uma grande variação entre as cultivares, entre as origens ecogeográficas, quanto às características biomassa da parte aérea, teor e concentração de N na parte aérea, e eficiência de uso (NUE), captação (NupE) e utilização (NutE) de N, especialmente em condições de HN. As cultivares do Noroeste da China apresentaram as maiores variações de biomassa, teor de N, NUE e NupE. Observou-se, ainda, uma forte correlação positiva entre NUE e NupE, e NUE e NutE, mas não houve correlação entre NupE e NutE. O NupE representou 77,6% da variação total do NUE, e o NutE representou o restante. A captação e a utilização de N apresentam grande variação entre cultivares de milheto no estágio de plântulas, e a variação da captação de N contribui mais do que a da utilização de N para a variação da eficiência de uso de nitrogênio.

Termos para indexação: *Setaria italica*, cultivares ecológicas, eficiência de absorção de nitrogênio.

Introduction

Foxtail millet, *Setaria italica* (L.) Beauv. – a self pollinating C_4 plant and one of the ten small-grained cereals (small millets) – is an important grain crop used as staple food in some regions of China, India, and Japan, and is grown for animal feed in the USA and Europe (Austin et al., 2006; Upadhyaya et al., 2011). Foxtail millet shows a small diploid genome, and has become a model plant for biofuel crops and genomic study for C_4 carboxylase pathway and short growing duration (Jia et al., 2013). It has been reported as tolerant to drought, salinity, and infertile soil, and thought to be environmentally friendly crop (Doust et al., 2009).

In the past years, the planting area of foxtail millet has declined seriously because of its low-grain yield (in comparison with other staple cereals) that can not meet the food demand by people (Vetriventhan et al., 2012). However, in recent years, grain yields of foxtail millet have raised substantially under breeders' effort (Diao, 2007). Nevertheless, cereal crops are inefficient in the use of N fertilizer, as about 33% only of the N fertilizer applied to the crop is recovered in aboveground plant biomass, at the end of the cropping season (Garnett et al., 2009).

In China, a large amount of external N input was used in order to achieve a higher-grain yield, which had caused a severe environment pollution and a low-N fertilizer use efficiency (NUE) (Peng et al., 2010; Chen et al., 2014a; Liu et al., 2019). Therefore, considerable researches and extension works were undertaken to improve the N use efficiency (Chen et al., 2014b; Hou et al., 2019). The use of foxtail millet cultivars with higher-NUE is an important approach for sustainable agriculture (Storer et al., 2018; Haegele et al., 2013; Chen et al., 2014b). Although a lot of research on the genetic differences in NUE have been reported for most cereal crops – including wheat, rice, maize, sorghum, and barley (Kant et al., 2011; Ju et al., 2015) –, they are not yet known for such differences in foxtail millet.

Seedling stage, as an important period of crop growth, determines the developing of crop production and final grain yield. Crops have been reported as poor users of both available N and applied N fertilizer at the seedling stage because of the poor synchronization between the availability of N and the demand for N (Liao et al., 2004), which results in the potential for significant N losses. Hence, it is very important to know how to settle the inconsistence between N availability and crop demand, and increase the N use efficiency, which could be achieved from using germplasm with higher-N uptake and utilization efficiency at early growing season (Pang et al., 2014).

However, the evaluation of highly nitrogen efficient cultivars, for physiological mechanism study and breeding in foxtail millet, is yet to be undertaken.

The objective of this work was to identify the genetic variation of foxtail millet (*Setaria italica*) cultivars from three ecogeographic origins of China, regarding the uptake and utilization of N in genotypes at the seedling stage, aiming at the genetic improvement of this crop.

Materials and Methods

The experiments were carried out in a greenhouse, in the Shandong Academy of Agricultural Sciences, in Ji'nan city, in the province of Shandong, China, from May 2016 to June 2016.

The experiment was carried out in a completely randomized design, with four replicates, and two N condition treatments: 0.2 mmol L^{-1} (low-N) and 6 mmol L^{-1} (high-N). Seventy-nine foxtail millet cultivars, from three ecogeographic origins, were evaluated as follows: 37 from North China (NC), a summer sowing region; 25 from Northwest China (NWCC), a spring sowing region; and 17 from Northeast China (NEC), a spring sowing region (Table 1). Seed of the cultivars were sown on 20 May 2016, in rectangular plastic pots with the following dimensions: 0.5 width, 0.4 m height and 0.8 m length, with permeable bottom; the pots were filled with 35 kg sand substrate of 1.28 g cm^{-3} bulk density. The substrate was washed with purified water to avoid the sticking of nutrients. Seed were sown in twelve rows in the pot at 15 kg ha^{-1} seeding rate. One week after sowing, the seedlings were thinned to the density of 60 plant per pot. The pots were watered once every two days with purified water according to their weight, in order to maintain the sand water content close to 70% of field capacity before seedling emergence. Plants were watered once with modified Hoagland nutrient solution (with different N content for two N treatments), every two days after emergence. Before the spraying of the nutrient solution, the pots

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were always watered enough with purified water to wash off the residual nutrient element.

The plants were grown in the greenhouse under 26-16°C as a mean day-night temperature and 70% RH, and 4 weeks after sowing, they were harvested. Shoots were separated from roots at the ground level, dried at 70°C for 48 hours and weighed. The oven-dried shoots were then ground into powder for measurement. The N concentration in the shoots was measured using the Kjeldahl method.

NUE was calculated as the ratio of shoot dry matter to the amount of supplied N, and multiplied a hundred percent. NupE was calculated by dividing the shoot-N content by the supplied N amount, and multiplied a hundred percent. The N utilization efficiency (NutE) was calculated as the ratio of shoot dry matter to the shoot-N content, and multiplied a hundred percent. The analyses of variance using the F-test, at 95% probability, with the Statistical Product and Service Solutions software (SPSS) were used to test the differences for shoot biomass, N content, N concentration, NUE, NupE, and NutE between cultivars and N treatments, and the coefficient of variation (CV%) was calculated. The contribution of variation in NupE and NutE to the variation in NUE was determined according to Bingham et al. (2012). All determinations were replicated three times in each sample.

Table 1. Foxtail millet (*Setaria italica*) cultivars from three ecogeographic origins in China.

Nº	Cultivar	Type	Locality	Nº	Cultivar	Type	Locality
1	Lujin1	NC	SD	41	Jingu29	NWC	SX
2	Lujin3	NC	SD	42	Qingzhenzhu	NWC	SX
3	Lujin5	NC	SD	43	Jinfen03	NWC	SX
4	Liaonong1	NC	SD	44	Jingu34	NWC	SX
5	Lugu1	NC	SD	45	Jingu41	NWC	SX
6	Lugu2	NC	SD	46	Jingu45	NWC	SX
7	Lugu3	NC	SD	47	Jingu46	NWC	SX
8	Lugu4	NC	SD	48	Jingu48	NWC	SX
9	Lugu5	NC	SD	49	Datong32	NWC	SX
10	Lugu6	NC	SD	50	Jingu39	NWC	SX
11	Lugu7	NC	SD	51	Longgu5	NWC	SAX
12	Lugu8	NC	SD	52	Longgu7	NWC	SAX
13	Lugu9	NC	SD	53	Longgu10	NWC	SAX
14	Lugu10	NC	SD	54	Longgu11	NWC	SAX
15	Ji8062-8	NC	SD	55	Shenshehuangmaogu	NWC	SX
16	Jigu12	NC	SD	56	Jinguoyin	NWC	SX
17	Jigu13	NC	SD	57	Neihuaguzi180	NWC	SX
18	Jigu14	NC	SD	58	Neixiaoxiangyu	NWC	SX
19	Jigu15	NC	SD	59	Yangu2	NWC	SAX
20	Gufeng1	NC	HB	60	Yangu12	NWC	SAX
21	Jigu20	NC	HB	61	Qingu3	NWC	SAX
22	Jigu24	NC	HB	62	Yannongjiazhong	NWC	SAX
23	Jigu26	NC	HB	63	Chigu7	NEC	IM
24	Jigu29	NC	HB	64	Chigu8	NEC	IM
25	Xiaoxiangmi	NC	HB	65	Longgu25	NEC	HLJ
26	Jixiang1	NC	HB	66	Longgu31	NEC	HLJ
27	Qingfenggu	NC	HB	67	Longgu32	NEC	HLJ
28	Baogu18	NC	HB	68	Longgu34	NEC	HLJ
29	Yugu3	NC	HN	69	Chaogu12	NEC	LN
30	Yugu4	NC	HN	70	Chaogu14	NEC	LN
31	Yugu8	NC	HN	71	Yangu16	NEC	LN
32	Yugu9	NC	HN	72	Gongai2	NEC	JL
33	Yugu13	NC	HN	73	Gongai5	NEC	JL
34	Yugu14	NC	HN	74	Gongai6	NEC	JL
35	Yugu15	NC	HN	75	Gongai8	NEC	JL
36	Yugu17	NC	HN	76	Gonggu60	NEC	JL
37	93-15	NC	HN	77	Gonggu65	NEC	JL
38	Jingu30	NWC	SX	78	Gonggu72	NEC	JL
39	Changgu4	NWC	SX	79	Gonggu75	NEC	JL
40	Changsheng4	NWC	SX				

NC, North China, summer; NWC, Northwest China; NEC, Northeast China; SD, Shandong province; HB, Hebei province; HN, Henan province; SX, Shanxi province; SAX, Shaanxi province; [(9)]IM, Inner Mongolia Autonomous Region; HLJ, Heilongjiang province; LN, Liaoning province; JL, Jilin province.

Results and Discussion

There were significant differences among N treatments, cultivars, and the interaction between them (Table 2). Shoot biomass, shoot-N content, and shoot-N concentration at the seedling stage ranged significantly among cultivars (Table 3). The cultivars also varied significantly for NupE, NutE, and NUE, which showed that there had a significant variation of shoot biomass and nitrogen use among the different foxtail millet cultivars.

Shoot biomass, N content, and N concentration increased from 0.12 g per plant, 1.39 mg per plant, and 1.17%, under LN condition, to 0.22 g per plant, 5.21 mg per plant, and 2.43%, respectively, under HN condition (Table 3). NUE, NupE and NutE, in response to N level application, decreased from 42.82 g g^{-1}, 49.70%, and 86.07 g g^{-1} under LN condition to 2.58 g g^{-1}, 6.21%, and 41.42 g g^{-1}, respectively, under HN condition. Similar results have been reported for pearl millet (Singh et al., 2010). Shoot biomass showed the highest coefficient of variation (CV), followed by shoot-N content, NUE, NupE, and NutE. Nitrogen concentration in the shoots showed the lowest CV, under both LN and HN conditions. The variation of NupE explained 77.6%, and NutE, 22.4%, of the variation in NUE. The contribution of NupE to NUE increased from 74.1% under LN to 81.1% under HN. The CVs of shoot biomass, shoot-N content, NUE, and NupE under HN supply also increased from LN to HN, whereas the CVs of shoot-N concentration and NutE were similar both under LN and HN. These results are indicative that HN supply was advantageous to increase the phenotypic variation of early growth and N uptake in foxtail millet, but had no effect on the variation of plant shoot-N concentration and N use among cultivars at the seedling stage.

The early growth (shoot biomass, N content, N concentration) and NUE were different among the three ecogeographic types (Table 4). There was interaction between ecogeographic types and N treatments. Shoot biomasses of the three ecogeographic types were similar under LN, while shoot biomasses of the NC summer type and NEC type were higher than those of the NWCC type under HN. In both N conditions, the ecogeographic types had the following results: the NWCC type showed the highest CV of shoot biomass, and the NEC type, the lowest one; the NEC type showed the highest-N content, and the NWCC type, the highest CV of shoot-N content. There were no differences in shoot-N concentration and CV among the three ecogeographic types under LN. The N type had the highest-N concentration and CV of N concentration under HN.

The NUE was lower in HN condition, in the three ecogeographic types, which ranged from 15.3 times (NEC), 15.6 times (NC) to 19.8 times (NWCC) (Table 5). Under LN, the NEC type had the highest NUE, NupE, and NutE, followed by the NWCC type; and the NC type had the lowest NUE and its components. The NWCC type had the highest CV of NUE and NupE, and the NC type had the highest CV of NutE. While under HN, the NEC type had the highest NUE, NupE, and NutE. The NWCC type had the highest CV of NUE and NupE; and the NC type had the highest-CV of NutE under HN. The contribution of NupE to NUE under the NWCC, NC, and NEC types was 81.8, 75.2, and 76.5%, respectively.

The NEC type had the highest shoot biomass under HN, as well as the highest N-content, the highest NUE, and the highest NupE under both LN and HN. The CV of these traits was the highest in the NWC type, which means that the cultivars of the NEC type were more vigorous, and the cultivar variation of the NWC type was wider for the early growth and nitrogen use.

Table 2. Analysis of variance of the F values for shoot biomass, shoot-N content, shoot-N concentration, nitrogen use efficiency, nitrogen uptake efficiency and nitrogen utilization efficiency of foxtail millet (*Setaria italica*) cultivars.

Source of variation	DF	Shoot biomass	Shoot-N content	Shoot-N concentration	NUE	NupE	NutE
N treatment (N)	1	152.34**	423.94**	4290.00**	1205.82**	1320.40**	4092.20**
Cultivar (C)	78	1.90**	1.42**	2.17**	1.18**	1.43**	2.12**
C×N	78	34.60**	132.46**	6.39**	14.84**	24.75**	3.33**

**Significant at 1% probability.

Table 3. Mean, range, and coefficient variation(CV) of shoot biomass, shoot-N content, shoot-N concentration, nitrogen use efficiency(NUE), nitrogen uptake efficiency(NupE), and nitrogen utilization efficiency (NutE) for 79 foxtail millet (*Setaria italica*) cultivars under low- (LN) and high- (HN) nitrogen conditions.

Characteristic	Mean		Range		CV (%)	
	LN	HN	LN	HN	LN	HN
Shoot biomass (g/plant)	0.12	0.22	0.05–0.20	0.09–0.40	35.39	50.83
Shoot-N content (mg/plant)	1.39	5.21	0.64–2.22	1.95–9.82	32.82	48.46
Shoot-N concentration (%)	1.17	2.43	0.98–1.39	2.05–2.89	11.52	11.22
NUE (g g^{-1})	42.82	2.58	17.74–70.54	1.01–4.73	35.35	50.61
NupE (%)	49.70	6.21	22.91–79.54	2.32–11.70	32.82	48.45
NutE (g g^{-1})	86.07	41.42	72.27–102.20	34.60–49.67	11.53	11.27

According to the means of shoot biomass, NUE, N content, NupE, N concentration, and NutE of under LN and HN, the 79 cultivars of the three ecogeographic types were divided into four types: higher than the means under LN and HN (HLHH); lower than the means under LN and HN (LLLH); higher than the means under LN and lower than the means under HN (HLLH); and lower than the means under LN and higher than the means under HN (LLHH) (Figure 1). The different cultivars described in the present study could provide useful materials for their inclusion in breeding programs aiming at the genetic improvement for N uptake and N utilization, and for exploiting the understanding mechanisms driving the genotypic variation for N uptake and N utilization.

Across all cultivars, NUE was positively correlated with its components NupE and NutE, and the difference of NupE contributed more to the variation in NUE than NutE (Figure 2). The results were in agreement with other studies showing that the variation in NUE among cultivars was associated with difference in NupE and NutE; they also showed that most of the variation in NUE among cultivars was associated with differences in NupE rather than NutE (Muurinen et al., 2006; Sylvester-Bradley & Kindred, 2009; Bingham et al., 2012). On this basis, shoot biomass was positively

Table 4. Mean, coefficient of variation (CV), and range of shoot biomass, shoot-N content, shoot-N concentration of cultivars from three eco-geographic types of foxtail millet (*Setaria italica*), under low- (LN) and high- (HN) nitrogen supply.

N rate	Ecogeographic regions	Biomass (g per plant)			N content (mg per plant)			N concentration (%)		
		Mean	CV (%)	Range	Mean	CV (%)	Range	Mean	CV (%)	Range
LN	NC	0.12a	31.82b	0.08–0.18	1.37b	29.31b	0.99–1.94	1.17a	11.68a	0.98–1.37
	NWC	0.12a	42.98a	0.05–0.20	1.39b	39.99a	0.64–2.18	1.17a	11.69a	1.03–1.32
	NEC	0.12a	29.22c	0.07–0.17	1.44a	29.48b	0.92–2.22	1.17a	11.61a	1.05–1.39
HN	NC	0.23a	48.22b	0.10–0.40	5.52b	45.67b	2.71–9.82	2.45a	12.20a	2.01–2.83
	NWC	0.18b	56.48a	0.09–0.31	4.43c	54.40a	1.95–7.60	2.44a	9.47c	2.13–2.71
	NEC	0.24a	42.98c	0.10–0.36	5.69a	40.31c	2.38–8.15	2.37b	11.22b	2.13–2.89
F_N		2,102.7**	1,453.1**		105,426.3**	8,007.1**		35,002.2**	273.43**	
F_C		60.63**	450.33**		1,159.2**	2,334.8**		12.26*	352.06**	
$F_{C'N}$		60.63**	5.90*		1,092.0**	109.68**		18.27**	361.13**	

*, **Significant at 5 and 1% probability, respectively. NC, North summer; NWC, Northwest; NE, Northeast.

Table 5. Mean, coefficient of variation (CV), and range of nitrogen use efficiency(NUE), nitrogen uptake efficiency (NupE), and nitrogen utilization efficiency (NutE) of foxtail millet (*Setaria italica*) cultivars (of three ecogeographic regions in China), under low- (LN) and high- (HN) nitrogen conditions.

N rate	Ecogeographic regions	NUE ($g\,g^{-1}$)			NupE (%)			NutE ($g\,g^{-1}$)		
		Mean	CV (%)	Range	Mean	CV (%)	Range	Mean	CV (%)	Range
LN	NC	42.00b	32.15b	27.68–65.77	48.78b	29.31b	35.24–69.36	86.09a	12.03a	72.85–102.20
	NWC	43.18ab	43.10a	17.74–70.54	49.82b	39.99a	22.91–77.84	86.35a	11.50b	75.65–97.42
	NE	44.07a	30.49c	25.60–60.12	51.52a	29.49b	33.01–79.45	85.63a	11.09c	72.27–95.69
HN	NC	2.70b	48.01b	1.23–4.73	6.57b	45.68b	3.23–11.70	41.09b	12.70a	35.33–49.67
	NWC	2.18c	56.29a	1.01–3.71	5.28c	54.38a	2.32–9.05	41.22b	9.51c	36.85–46.99
	NE	2.88a	42.20c	1.14–4.31	6.77a	40.30c	2.83–9.70	42.43a	10.29b	34.60–46.88
F_N		55,733.8**	1,284.4**		63,434.0**	8,101.7**		15,797.3**	197.90**	
F_{CT}		15.15**	440.47**		34.80**	2,362.2**		0.51^{ns}	551.13**	
$F_{CT'N}$		12.27*	10.26*		21.96**	111.29**		3.11^{ns}	234.23**	

*, **Significant at 5 and 1% probability, respectively. NC, North China, summer; NWC, Northwest; NEC, Northeast.

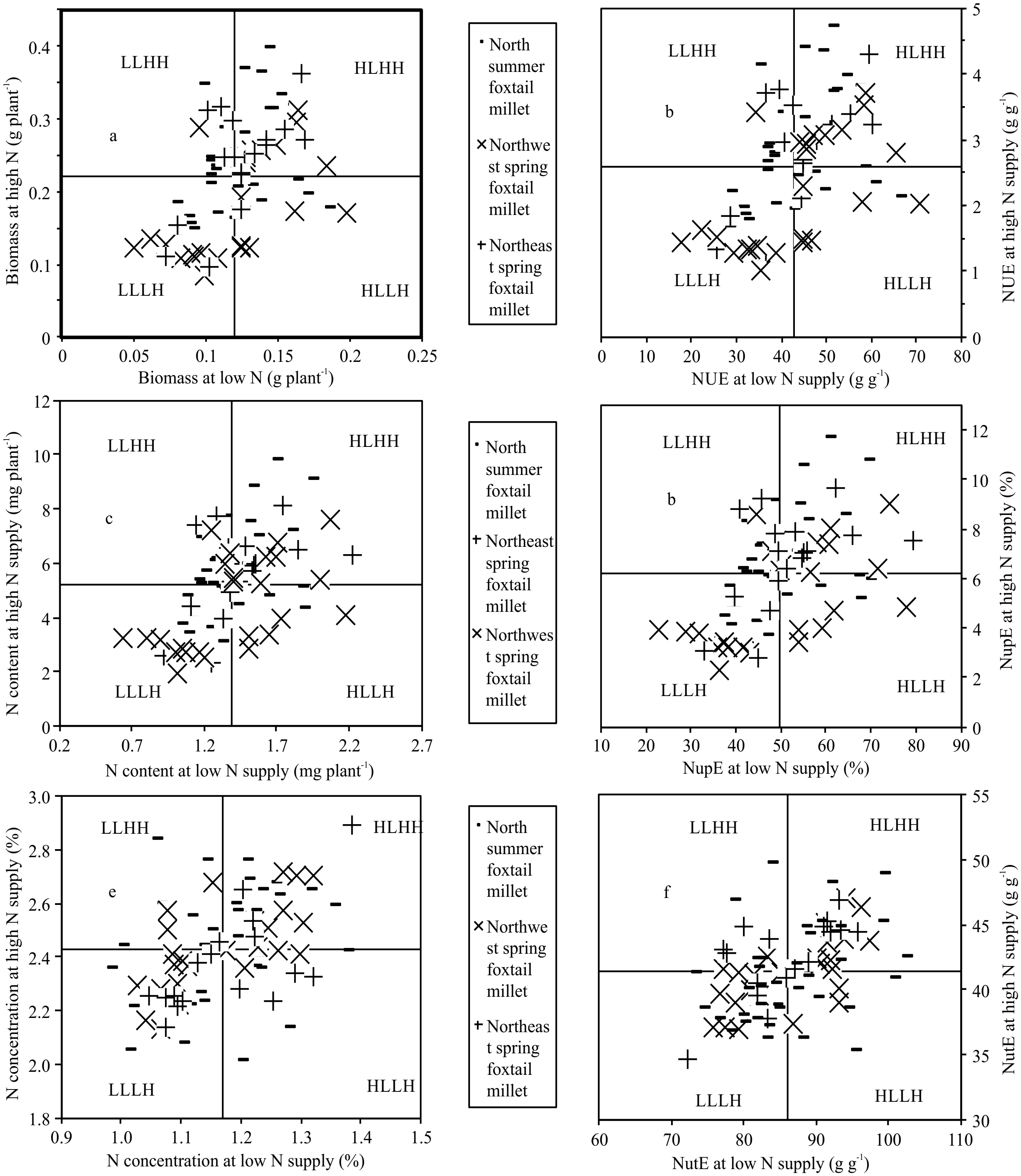

Figure 1. Classification of cultivars of three ecogeographic types, in China, according to the following means for: A, biomass; B, nitrogen use efficiency (NUE); C, N content; D, nitrogen uptake efficiency (NupE); E, N concentration; and F, nitrogen utilization efficiency (NutE) under low-nitrogen (LN) and high-nitrogen (HN) conditions. HLHH, higher than the means both under LN and HN; LLLH, lower than the means both under LN and HN; HLLH, higher than the mean under LN, and lower than the mean under HN; LLHH, lower than the mean under LN, and higher than the mean under HN.

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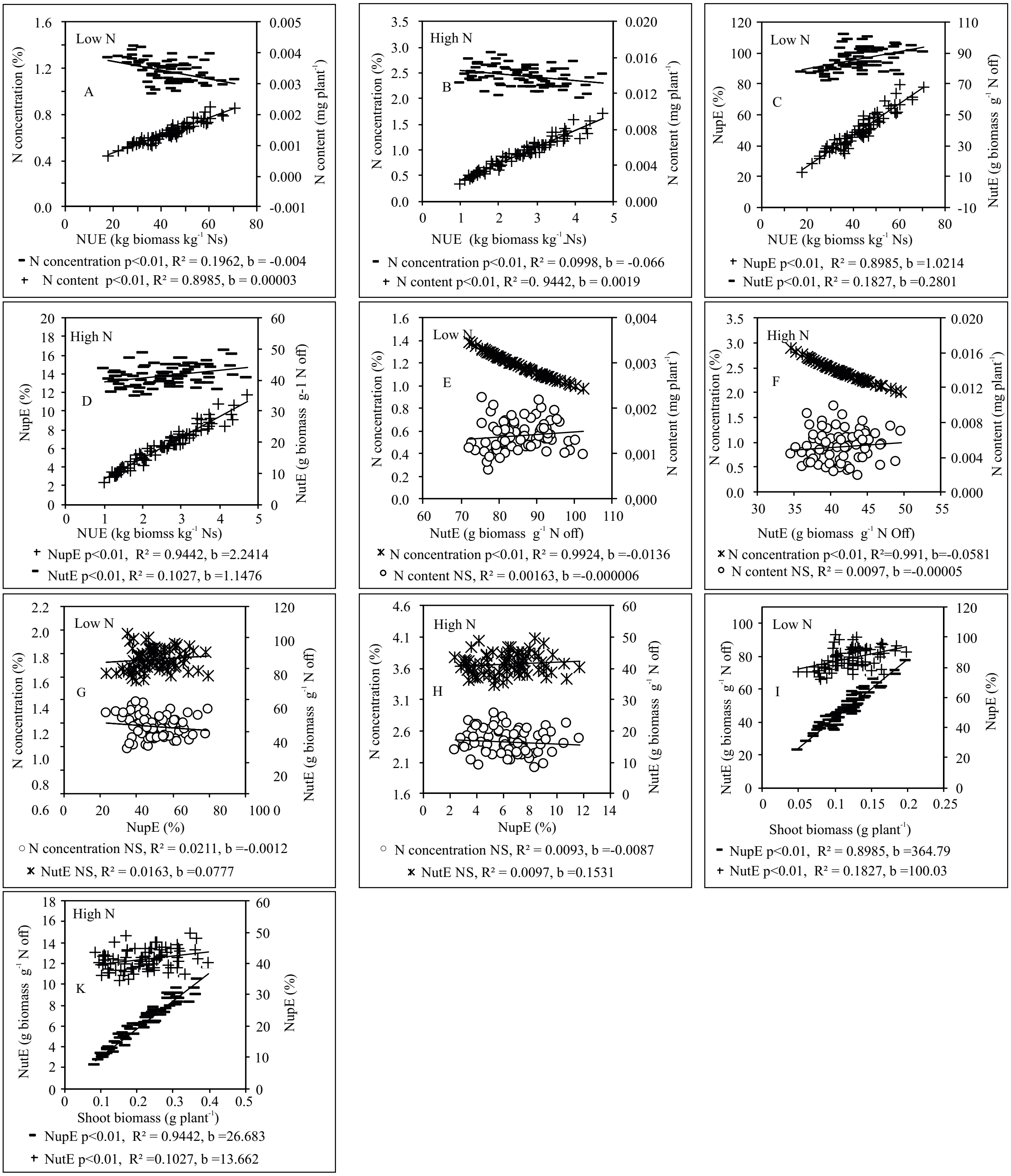

Figure 2. Relationship between the following parameters under low-nitrogen (LN) and high-nitrogen (HN) conditions: nitrogen efficiency use (NUE) with N concentration and N content under LN (A) and HN (B); NUE with its components nitrogen uptake efficiency (NupE) and nitrogen utilization efficiency (NutE) under LN (C) and N (D) conditions; N concentration with N content and NutE among cultivars under LN (E) and HN (F); NupE with shoot N concentration and NutE under LN (G) and HN (H); shoot biomass with NupE and NutE under LN (I) and HN (K). Lines fitted by linear regression (y= a+bx) to mean values for individual cultivars. NSNonsignificant.

correlated with NupE and NutE in the present study. The correlation expresses the importance of N uptake and utilization for early plant growth, which was consistent with studies on wheat (Liao et al., 2004; An et al., 2006). NUE was positively correlated with N content, and negatively correlated with N concentration. By this result, it can be inferred that the cultivar with high-NUE should have high-N content and low-N concentration in the seedling stage of foxtail millet. There was no significant correlation between N content and NutE, and between N concentration and NupE, and also between NutE and NupE, which indicates that the improvement of N uptake and N utilization should be selected independently, and that the N content and N concentration should be avoided as selection criteria for NutE and NupE, respectively.

Conclusions

1. There is a large variation for shoot biomass and nitrogen use efficiency among foxtail millet cultivars, from three ecogeographic origins of China, at the seedling stage, especially for high-N levels.
2. Northwest type cultivars show the highest variation of shoot biomass, N content, N concentration, nitrogen use efficiency and nitrogen uptake efficiency than the Northeast and NC types, at seedling stage.
3. There is a large variation for nitrogen uptake and nitrogen utilization among foxtail millet cultivars; and the variation of nitrogen uptake contributes more than that of nitrogen utilization to the variation of nitrogen use efficiency.

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