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Varietal differences in root growth as related to nitrogen uptake by sorghum plants in low-nitrogen environment

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Key words: hybrid, local, N absorption rate, semi-arid tropics (SAT), sorghum, specific N absorption rate in roots

Abstract

Hybrid (*Sorghum bicolor* (L.) Moench cv CSH 9) and local variety (*S. bicolor* cv. FSRP) of sorghum were grown in an Alfisol field and in pots of Alfisol in semi-arid tropical India, and the productivity of sorghum in low N condition was studied in relation to N absorption by plant. The grain yield of the hybrid (CSH 9) was higher than that of the local variety (FSRP) irrespective of the rate of N application. The reduction in hybrid grain yield was less than that for the local variety when N was not applied. After booting stage hybrid absorbed more N than the local variety. To estimate the role of roots in N absorption, the characteristics of N absorption were parameterized. Relative growth rate was highly correlated with relative N absorption rate in plant. N absorption was regulated by root activity (specific N absorption rate per unit root mass and length). Specific N absorption rate in roots at physiological maturity was higher in the hybrid than in local variety in low N conditions. Therefore, the smaller reduction of hybrid yield in low-N conditions was ascribed to high-N absorption rate in its roots, and the high ability of roots to absorb N after booting stage.

Introduction

Sorghum is widely grown in the semi-arid tropics (SAT), where various types of stress exit. Nutrient – especially nitrogen (N) and phosphorus- and drought stresses are the most important factors affecting productivity (Marschner, 1995; Osaki et al., 1992). Nitrogen is the most limiting nutrient in Alfisol of the SAT because of their low organic matter, high losses of nitrogen through various mechanisms, and immobilization in the soil (Das and Chatterjee, 1982; Khanna et al., 1982; Prasad and Thomas, 1982).

The development and release of hybrids and high-yielding varieties of sorghum have led to a substantial increase in the yield of sorghum under N-limiting condition in SAT areas (Doggett et al., 1970; Martin, 1970; Rachie, 1970; Rao, 1982), suggesting that some hybrids and improved varieties are adapted to limited-N condition.

The ability of crop plants to use the mineralized-N depends on the root system development and the rate at which they absorb N (Lee et al., 1996; Rao et al., 1993). It was reported that, in vegetative stage, the rate of N accumulation by plant was regulated by the N absorption rate in several cereal crops (Osaki et al., 1995; Shinano et al., 1994). However, these results were observed in adequate N level, not low-N level, and the effect of low-N environment on the relationship between N absorption and production and N accumulation in plant was still unclear. Thus, it was assumed that effective N absorption from soils is one of the mechanisms by which sorghum is adapted to low-N conditions and that sorghum hybrids could have the ability to absorb more nutrients from low-nutrient soils in SAT than the local varieties.

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Table 1. The size and N concentration of the seeds sown in the field and pot experiments, ICRISAT, Patancheru, India, rainy season, 1996 and 1997

	Seed size ($mg\ seed^{-1}$)		N concentration ($g\ N\ kg^{-1}$)	
CSH9	27.6	(0.6)	11.4	(0.6)
FSRP	31.1	(0.3)	15.4	(0.7)

Numbers in parentheses are standard errors

A number of genotypes of sorghum were evaluated in low-N condition to assess the extent of genotypic variation among cultivars and identify physiological traits. Biomass, grain yield and N uptake in plant were highest in the hybrids and improved cultivars compared to local varieties in sorghum (Adu-Gyamfi et al., 2002; Nakano et al., 2002). Based on their results, we selected a hybrid (CSH 9) and local variety (FSRP), which have been commonly cultivated in farmers' field in India. Field and pot experiments were conducted to compare the physiological basis of growth and dry matter production in a hybrid (CSH 9) and a local variety (FSRP) of sorghum in low-N condition by examining the relationship between root growth and N-absorption rate.

Materials and methods

Field experiment

The experiment was conducted during 1996 rainy season on an Alfisol at ICRISAT, Patancheru, India. Hybrid sorghum (*Sorghum bicolor* L. Moench) cv. CSH 9 and local variety FSRP were sown on 25 June 1996. The size and N concentration of the seeds used in field experiment is shown in Table 1. The timings of growth stage (booting and growth period, etc.) in both genotypes were almost same at previous experiments (Adu-Gyamfi et al., 2002; Nakano et al., 2002). Spacing was 60 × 10 cm. Two levels of N fertilizer, 0 [0N] and 100 kg N ha^{-1} [100N] as urea were applied before sowing. All plots received a uniform basal application of 20 kg P ha^{-1} as single superphosphate. The experiment layout was a randomized block design with three replications. The size of each plot was 5 × 6 m. Annual rainfall was 1063 mm, with 1000 mm between June and October. The mean temperature was 26.8 °C between June and October.

Samples (six to 10 plants) were taken at about 21-day intervals after emergence. Samples were separated into leaves, stems, roots, and panicles. Samples were oven-dried at 80 °C for 48 h, ground, dry weights determined, and a portion of the ground material used for N analysis. In addition, samples (80–110 plants) were taken at final harvest and grain yield was determined.

A monolith sampling methods was used to collect roots in the soil to 60 cm depth. Roots were washed in mesh net in the tap water to remove the soils, and the total root lengths were determined with a COMAIR root scanner (Devi et al., 1996).

Pot experiment

A hybrid (CSH 9) and local variety (FSRP) of sorghum were grown in 10-l pots (one plant per pot) contained 10 kg Alfisol soil during 1997 rainy season in the greenhouse at ICRISAT, Patancheru, India. The size and N concentration of the seeds used in pot experiment is shown in Table 1. Nitrogen was supplied by basal application of urea at two levels; 0 g N pot^{-1} (-N) and 2 g N pot^{-1} (+N) (Shinano et al., 1991). Phosphorus was applied at 2 g P_2O_5 pot^{-1} as single superphosphate. Pots were irrigated with water during the experiment to maintain 60% maximum water holding capacity. The mean temperature of greenhouse during experiment was 25 °C. The experiment layout was a randomized block design with three replications.

Plants were sampled at vegetative, booting, physiological maturity, and final harvest stages. Twelve plants were sampled at each sampling time. Samples were separated into leaves, stems, roots, and panicles. The dry weight samples were determined after they had been oven-dried at 80 °C for 48 h. Samples were ground and a portion of the ground material used for N analysis.

Measurement

Nitrate in the soil was determined in dried soil after extraction with KCl (Keeney and Nelson, 1982), total N by Kjeldahl's method. The N-status and pH of soil used in field and pot experiments is shown in Table 2. The N concentration in samples was analyzed by indophenol color formation (Chaykin, 1969) after digestion with a hydrogen peroxide–sulfuric acid mixture (Singh et al., 1984).

N absorption rate in the plant (AR) was calculated from total amount of N absorbed in whole plant using the following equation:

$$AR = (N_1 - N_2)/(t_1 - t_2),$$

Table 2. Nitrate-N concentration and total N in field soil and pot soil before fertilizer application, ICRISAT, Pantancheru, India, rainy seaseon 1996 and 1997, respectively

		Field		Pot	
$pH(H_2O)$		6.26	(0.11)	6.69	(0.02)
NO_3-N	(mg kg^{-1} soil)	2.93	(0.99)	5.83	(0.24)
Total N	(g kg^{-1} soil)	0.60	(0.09)	0.39	(0.01)

Numbers in parentheses are standard errors.

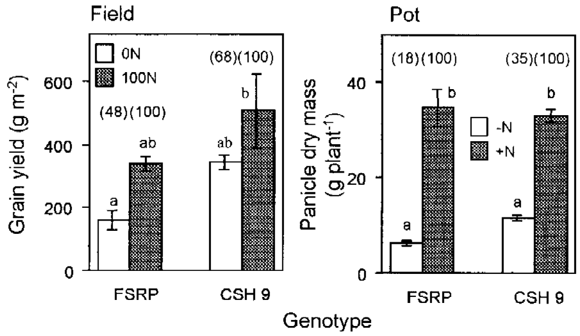

Figure 1. Grain yield in the field experiment, and panicle dry mass in pot experiment of a sorghum hybrid (CSH 9) and a local variety (FSRP), ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. Values in parentheses are the relative values compared to the 100N treatment in the field experiment and +N treatment in pot experiment. The vertical bars indicate ±SE. Bars with the same letter indicate no significant difference at p=0.05 level.

where: N_1 is the total N absorbed in the plant at t_1, N_2 the total at t_2; t is the number of days after emergence. The relative N absorption rate in whole plant (RAR) was calculated as AR divided by total dry mass in whole plant.

To estimate the role of root in N absorption, RAR was studied with parameter analysis related to root activity and distribution ratio of dry mass to roots as follows:

$$RAR = SAR \times FWR, \quad (1)$$

where: SAR is specific absorption rate of N per roots mass, and FWR is the distribution ratio of dry mass to roots (the ratio of root dry mass to whole plant dry mass). In addition, SAR was parameterized into specific absorption rate of N per root length (SARL) and specific root length (SRL) as follows:

$$SAR = SARL \times SRL \quad (2)$$

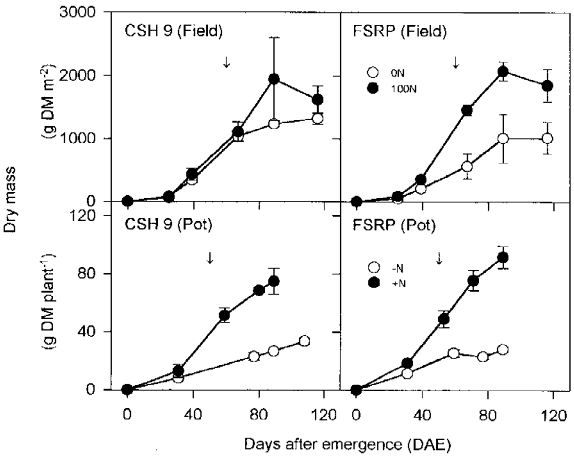

Figure 2. Amount of dry mass accumulated in whole plant at successive growth stages of a sorghum hybrid (CSH 9) and a local variety (FSRP) in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. The arrow in the figure indicates the booting time. The vertical bars indicate ±SE.

Results

Yield

In the field experiment, the grain yield of the hybrid CSH 9 was higher than that of local variety FSRP (Figure 1). The grain yield of 0N treatment was 68% of 100N grain yield in the hybrid, while in the local variety, grain yield of 0N treatment was 48% of grain yield of the 100N treatment. In the pot experiment, the dry mass of panicle of −N was 35% of panicle dry mass of +N in hybrid, while dry mass of panicle of −N was 18% of panicle dry mass of +N in local variety. There was the smaller reduction in yield and panicle dry mass in the hybrid than in the local variety when no N was applied.

Accumulation of dry mass and N in plants

In the field experiment, the growth in 100N was larger than that in 0N in hybrid and local variety (Figure 2). The difference in the growth between 100N and 0N treatments in hybrid was smaller than that in local variety. In the pot experiment, the difference in the growth between +N and −N treatments also was smaller in hybrid than in local variety. Dry mass of whole plant in hybrid increased after the booting stage in −N treatment, while dry mass of whole plant in local variety remained constant after the booting stage in −N treatment.

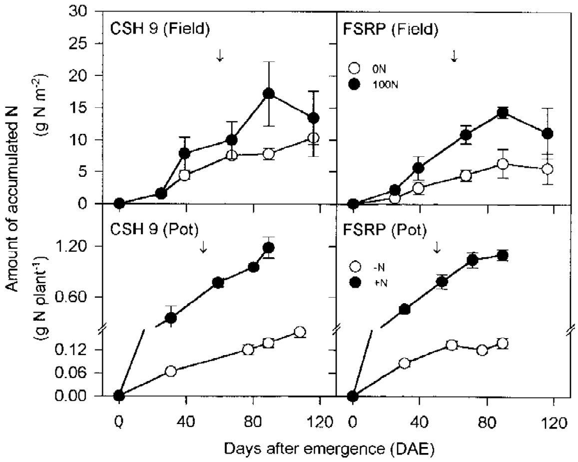

Figure 3. Amount of N accumulated in whole plant of a sorghum hybrid (CSH 9) and a local variety (FSRP) at successive growth stages in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. The arrow in the figure indicates the booting time. The vertical bars indicate ±SE.

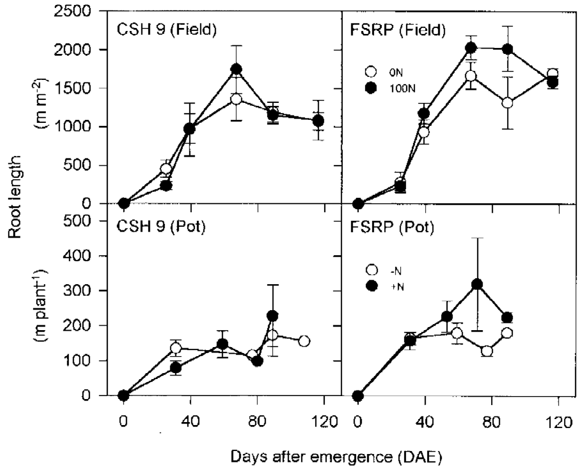

Figure 5. Root length at successive growth stages of a sorghum hybrid (CSH 9) and a local variety (FSRP) in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. The vertical bars indicate ±SE.

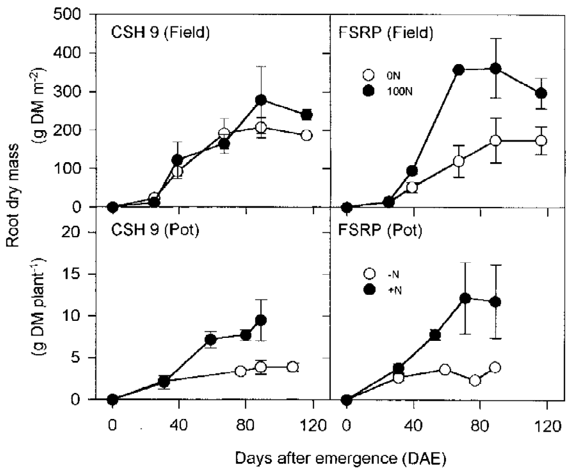

Figure 4. Root dry mass at successive growth stages of a sorghum hybrid (CSH 9) and a local variety (FSRP) in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. The vertical bars indicate ±SE.

In the field experiment, the amount of N absorbed by hybrid plants increased after the booting stage in both N treatments, but the amount of N absorbed by plants of local variety in 100N treatment remained constant after booting (Figure 3). The amount of N absorbed in plants of local variety at 0N in the field experiment did not increase after booting stage. In the pot experiment, the amount of N absorbed by hybrid plants increased continuously after booting stage in both N treatments, but the increase of amount of N absorbed in plants of local variety was slowed down after booting stage in +N treatment. The amount of N absorbed in plant of local variety did not increase after booting stage in −N treatment.

Root growth

Root dry mass increased with fertilizer-N, while root length was not much affected by fertilizer-N in hybrid and local variety (Figures 4 and 5). The reduction of dry mass and length of roots were larger in local variety than that in hybrid when no N was applied in the field and pot experiments.

Relative N absorption rate (RAR), specific absorption rate of N per root weight and length (SAR, SARL), distribution ratio of dry mass to root (FWR), specific root length (SRL)

In the field and pot experiments, FWR was not correlated to RAR, but SAR was highly correlated with RAR in both genotypes (Figure 6). In addition, SRL was not closely correlated with SAR, but SARL was highly correlated with SAR (Figure 7). In Table 3, regression between relative growth rate (RGR) and each parameter that depend on N absorption were shown. RGR was correlated with RAR, SAR, FWR and SARL in both experiments.

Table 3. Correlation of relative N absorption rate in whole plant (RAR), specific absorption rate of N per roots mass (SAR), distribution ratio of dry mass to roots (FWR), specific absorption rate of N per root length (SARL), and specific root length (SRL) with relative growth rate in plant

	RAR	SAR	FWR	SARL	SRL
Field experiment	0.94**	0.77**	0.61*	0.81**	0.76**
Pot experiment	0.82**	0.76**	0.65**	0.52*	0.30

*Significant at 5% level; **significant at 1% level.

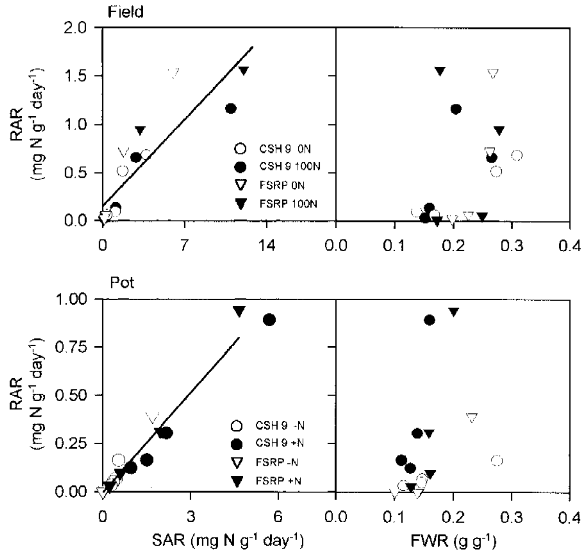

Figure 6. Relationship between relative absorption rate of N (RAR), specific absorption rate of N per root mass (SAR), and the ratio of root dry mass to whole plant dry mass (FWR) of a sorghum hybrid (CSH 9) and a local variety (FSRP) at successive growth stages in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. The regression slope is represented by RAR=0.128SAR+0.150 (r^2=0.771, p<0.01) in the field experiment and RAR=0.174SAR-0.006 (r^2=0.955, p<0.01) in the pot experiment.

RAR, SAR, and SARL at the physiological maturation stage

The RAR, SAR, and SARL tended to be higher in the hybrid than local variety irrespective of N level in both field and pot experiments at physiological maturity (Table 4). The ability of roots to absorb N remained higher in the hybrid than local variety during maturation.

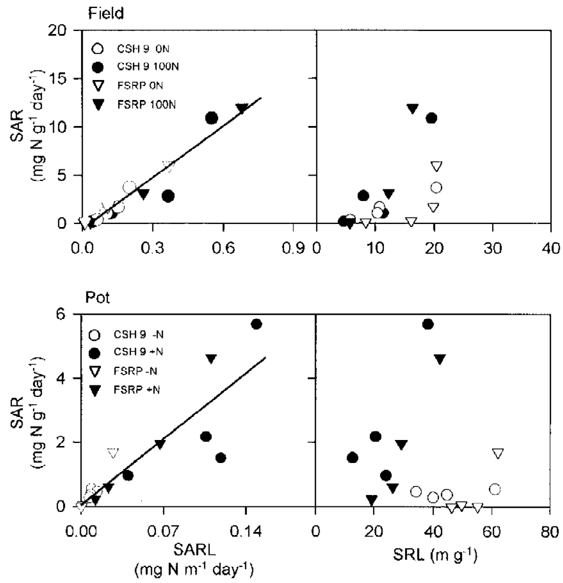

Figure 7. Relationship between specific absorption rate of N per root mass (SAR), specific absorption rate of N per root length (SARL) and specific root length (SRL) of a sorghum hybrid (CSH 9) and a local variety (FSRP) at successive growth stages in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively. The regression slope is represented by SAR=17.9SARL–0.597 (r^2=0.927, p<0.01) in the field experiment and SAR=29.3SARL+0.058 (r^2=0.774, p<0.01) in the pot experiment.

Discussion

The present study focused on the physiological mechanism of sorghum for adaptation to limited N conditions, for which a little information is available. The yields of hybrid (CSH 9) were higher than that of local variety (FSRP) in field experiment (Figure 1). The reduction in yield of the local variety was larger than that of hybrid when no N was applied in both field and pot experiments. These data suggest that the hybrid was more adapted to limited-N conditions than local variety. It is known that seed vigor and viability are important components influencing seedling establishment, crop growth, and productivity (TeKrony and Egli, 1991; Welch, 1986) and that seeds with low nutrient reserves are disadvantaged unless sown to soils with adequate available nutrients for seedling establishment and growth after germination (Welch, 1986, 1999). The size and N concentration of the seeds sown in our experiments were larger in local variety than in hybrid (Table 1). Thus, the difference in the results between hybrid and local variety would not be due to the size and N concentration of the seeds used in our experiments. The amount of N absorbed by plants

Table 4. Relative absorption rate of N of sorghum in whole plant (RAR), specific root absorption rate of N per root weight (SAR), and specific root absorption rate of N per root length (SARL) at physiological maturity of sorgum hybrid (CSH 9) and local variety (FSRP) in field and pot experiments, ICRISAT, Patancheru, India, rainy season 1996 and 1997, respectively

Genotype	N treatment	RAR (μg N g^{-1} day^{-1})	SAR (μg N g^{-1} day^{-1})	SARL (μg N m^{-1} day^{-1})
Field experiment				
CSH 9	0N	64.7^{b}	377^{b}	62.8^{c}
FSRP	0N	21.6^{a}	133^{a}	12.6^{ab}
CSH 9	100N	30.8^{ab}	202^{ab}	43.2^{bc}
FSRP	100N	9.3^{a}	53.2^{a}	9.5^{a}
Pot experiment				
CSH 9	−N	52.4^{xy}	368^{xy}	8.2^{xy}
FSRP	−N	0.8^{x}	8.3^{x}	0.2^{x}
CSH 9	+N	165^{yz}	1507^{y}	118^{y}
FSRP	+N	98.2^{y}	613^{xy}	23.3^{xy}

Field experiment and pot experiments analyzed separately. Values followed by the same letter in the same column are not significantly different at P=0.05.

increased in hybrids after the booting stage (Figure 3). Furthermore, in low-N condition, the amount of N absorbed in plants increased in hybrids, but did not increase in the local variety after booting stage. The N absorption rate remained high in the hybrid, especially in low-N conditions, and this continuous absorption of N may have contributed to the higher yields of the hybrids (Osaki et al., 1991, 1995). Thus, it is suggested that the ability of roots to absorb N after the booting stage play an important role in controlling grain and dry matter production in sorghum.

Root dry mass was affected by N-treatments but root length was not much (Figures 4 and 5). This observation is consistent with that of Lee et al. (1996), who also reported that 0N application reduced root biomass, not root length. Myers (1980) reported that shoot biomass varied with fertilizer levels, but root biomass did not, suggesting that the ratio of root biomass to whole plant dry mass is affected by fertilizer levels. Brown et al. (1987) observed fertilizer-N had little effect on the ratio of roots to total plant weight of barley, which indicated that root biomass production responded to fertilizer in a similar way to above-ground biomass production. In this study, the similar responsiveness of the root biomass and the above-ground biomass production would be supported by little difference of the range of FWR in fertilizer-N levels (Figure 6).

The plants showed a close relationship between amount of absorbed N in plant and dry mass in plant and plant growth was substantially regulated by the amount of absorbed N in plant (Nakamura et al., 1997; Osaki et al., 1992; Shinano et al., 1994). Thus, N absorption rate may affect the plant growth rate. To evaluate the role of roots in N absorption, each parameter was estimated by based on Eqs. (1) and (2) and correlation between each parameter and relative growth rate (RGR) was analyzed (Table 3). RAR, SAR, FWR and SARL was closely related to RGR in both experiment, especially regression coefficients of RAR-RGR and SAR-RGR were higher than the others, which indicated plant growth rate would be regulated by N absorption rate. Nutrient absorption is controlled by root size in plant (Haynes et al., 1991; Iwama, 1988). On the contrary, it is reported that nutrient absorption by plant is controlled by root activity (e.g., nutrient absorption rate of roots) (Hilbert, 1990; Takahashi et al., 1991). In seven crops, root biomass was not related to nitrogen absorption or dry mass production especially during maturation (Osaki et al., 1995, 1997). SAR was strongly correlated with RAR, and SARL was strongly correlated with SAR (Figures 6 and 7). These results indicated that N absorption rate per root dry mass and length regulated N absorption rate in whole plant.

RAR, SAR, SARL at the physiological maturity were higher in the hybrid than in the local variety irrespective of N treatments (Table 4). In the hybrid, N was absorbed continuously after booting stage (Figure 3). This ability of high N absorption in hybrid was due to its high SAR and SARL (Figures 6 and 7). High-N absorption by roots after the booting stage in sorghum would be an important physiological trait for high productivity in low-N environment.

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