CHAPTER 7

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The effect of plant population and nitrogen fertilization on the growth, yield and nitrogen use efficiency of sorghum in semi-arid areas in Ethiopia

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An experiment was conducted at two locations in NE Ethiopia to determine the effect of population density on the growth, yield and nitrogen use efficiency of sorghum under different levels of nitrogen fertilizer. Eight treatments, which consisted of factorial combinations of two N fertilizer levels (0 and 80 kg ha^{-1}) and four population densities (166 666, 88 888, 38 095 and 29 629 plants ha^{-1}), were evaluated in a randomised complete block design with three replications. The results indicated that nitrogen fertilizer significantly enhanced leaf area index, dry mass production, crop growth rate, and panicle and grain yields. Nitrogen fertilizer also positively affected yield components. Leaf area index, plant height and crop growth rate (at the early growth stages) as well as leaf, stem, panicle and total dry mass production increased as population density increased. Grain, panicle and stover yields at harvest increased in linear responses to increase in population density. Head and seed number per unit area accounted for most of the variation in grain yield at different plant densities. Stover and grain N concentrations and grain protein concentration increased with a reduction in population density, while N uptake increased with increasing population density. It can be concluded that the conventional planting density (88 888 plant ha^{-1}), being used in NE Ethiopia is not optimal for high grain yield, as increases in grain yield were linear up to a population density of 166 666 plants ha^{-1}. Thus, further study to determine the optimum planting density is recommended.

Keywords: grain yield, nitrogen fertilization, population density, sorghum

Introduction

A prerequisite for growing a successful sorghum crop is to obtain an adequate plant population density (Ismail & Ali, 1996). In areas where crop growth is constrained by limited precipitation optimising planting density is critical as high population densities may deplete most of the available moisture before the crop matures, while low densities may leave moisture unutilised (Reddy & Reddi, 1992).

Plant density strongly affects LAI, and therefore light interception and canopy photosynthesis (Gan *et al.*, 2002). In most crops planting density is a major management tool for increasing the capture of solar radiation. Van Averbeke & Marais (1992) and Cox (1996) indicated that higher LAI values, obtained by increasing planting density, resulted in higher crop growth rates during grain filling, and consequently, in higher grain yields. The influence of plant population density on grain sorghum canopy architecture, light interception and grain yields has been extensively recorded. Several scientists (Blum, 1970; Kudasomannavar, Kulkarni & Patil, 1980; Tetio-Kagho & Gardner, 1988; Amano & Salazar, 1989; Ogunlela & Okoh, 1989; M'Khaitir & Vanderlip, 1992) reported the development of higher leaf area indices and thus better radiation interception and radiation use efficiency with higher population densities. This ultimately results in higher yields under favourable growing conditions. In the absence of constraints from other environmental factors, crop productivity may be limited by the intercepted light (Ma, Dwyer & Costa, 2003).

There is a lack of recent research information on sorghum production practices in NE Ethiopia. Yield-density relationships for sorghum have not been studied in most of the sorghum growing areas. In areas where sorghum growth and yield is often constrained by limited and erratic rainfall, production strategies to use stored soil water and limited seasonal precipitation efficiently include, amongst others, the choice of plant population density. The objective of this study was, therefore, to determine the influence of plant population density on the growth, yield and nitrogen use efficiency of sorghum at different levels of nitrogen fertilization under the semi-arid conditions of NE Ethiopia.

Materials and Methods

Study sites

The experiment was conducted at Sirinka (11^0 45' N latitude, 39^0 36' E longitude; 1890 m. a. s. l. altitude) and Kobo (12^0 9' N latitude, 39^0 38' E longitude; 1470 m. a. s. l. altitude) research sites in NE Ethiopia under rainfed conditions during the 2002 growing season. The soil type at both locations was a Eutric vertisol. Details of the physicochemical characteristics of the soils are presented in Appendix Table 7.1. Climatic conditions in the growing season, at both locations, are presented in Table 1. Rainfall received in the growing season was similar to the long term average at Sirinka and above the long term average at Kobo. The relatively high total seasonal rainfall can be misleading, as great variability in distribution often exists. For instance, in this particular season about 78% and 76% of the rainfall at Sirinka and Kobo, respectively, was concentrated in July and August. The growing season at both experimental sites, and at Kobo in particular, is characterized by high temperatures, the maximum being above 25^0 C for most of the time (Table 1).

Table 1 Monthly precipitation and air temperatures during the growing season at the two locations

	Sirinka				Kobo			
	Precipitaion (mm)		Temperature (^{0}C)		Precipitaion (mm)		Temperature (^{0}C)	
Month	2002	Long term*	Max.$^\varphi$	Min.$^\Re$	2002	Long term*	Max.$^\varphi$	Min.$^\Re$
July	229.5	192.1	30.5	17.1	99.8	108.2	34.0	19.6
August	280.6	266.3	27.8	15.7	296.0	200.4	30.9	17.6
September	134.0	95.0	26.6	14.7	112.4	95.2	29.9	15.7
October	12.0	57.7	26.6	12.4	16.0	43.7	30.5	13.0
November	0.0	21.7	25.5	11.6	0	11.9	29.5	12.0
Total	656.1	632.8			524.2	459.4		

* Long term average rainfall (1980-2002 for Sirinka and 1973-2002 for Kobo). $^\varphi$Maximum. $^\Re$Minimum.

Experimental design and procedure

The experiment at both sites was conducted in a completely randomized block design with three replications. Treatments consisted of factorial combinations of two N fertilizer levels (0 and 80 kg ha^{-1}) and four plant population densities (166 666, 88 888, 38 095 and 29 629 plants ha^{-1}). Sorghum was planted on flatbeds at Sirinka and in tied-ridges at Kobo. Urea was used as the N source. All plots received P as triple super phosphate at the rate of 20 kg P ha^{-1}.

All the P, and half of the N, were applied in a band at planting. The remaining N was side dressed at the six to eight leaf stage. In all cases fertilizers were incorporated into the soil. The newly released sorghum cultivar ICSV111 was hand drilled in 75 cm rows and thinned to the appropriate population densities. Gross plot size was 6 m wide by 5 m long. Hand weeding and insect control were conducted on an as needed basis. Prior to planting, composite surface (0-15 cm) and subsurface (15-30 cm) soil samples from nine points across the experimental field were collected and analyzed for soil physicochemical properties following the procedure outlined by Page, Miller & Keeney (1982).

Panicle length and seed weight and seed number panicle^{-1} were determined on four tagged plants in each plot. Three plants, representative of the plot, were harvested at 42, 63, 84, 105 and 115 DAE at Sirinka and 48, 69, 90 and 101 DAE at Kobo. These were separated into leaf, stalk (plus leaf sheath) and panicle fractions including all senescent leaf material. The plant components were dried in a forced-air oven at 80^0 C until constant weight was achieved. The length and breadth of green leaf was measured from which leaf area was calculated as the product of leaf length, maximum leaf breadth, and a shape factor of 0.75 (Oosterom, Carberry & Muchow, 2001).

Mean crop growth rate (CGR) and leaf area indices were calculated according to Hunt (1990). Three rows, after discarding border rows, were hand harvested to determine stover, total aboveground biomass and grain yield at maturity. Stover yield included the leaf, stalk and chaff component of the plant. Total aboveground biomass yield was determined as the sum of stover and grain yields. Panicles were air-dried, hand threshed and grain yield determined at 12.5% moisture content. Grain and stover samples were ground separately to pass through a 1 mm sieve. N content in plant samples was determined by the micro-Kjeldahl method (Page *et al*., 1982). N uptake in the grain and stover was calculated by multiplying the concentration with grain and stover yields respectively. Whole plant N uptake was calculated by adding the uptake in grain and stover. Grain protein concentration was calculated as %N in the grain x 6.25 (Kudasomannavar *et al*., 1980) and grain protein yield as (grain protein concentration x grain yield)/100 (Ogunlela & Okoh, 1989). Nitrogen harvest index (NHI) was calculated as the ratio of grain N uptake to whole plant N uptake.

Analysis of variance for the measured parameters was performed using the MSTATC statistical program (MSTATC, 1989). Whenever treatment differences were found to be significant, based on results of the *F*-test, critical differences were calculated at the 5% level of probability using Duncan's Multiple Range Test.

Results and Discussion

Leaf area index

Increasing population density resulted in an increase in LAI at both sites (Figure 1A & B). The increased LAI at higher densities was because of the presence of more plants per unit area. This result agrees with the results of Amano & Salazar (1989) who reported increased LAIs with increasing population densities in sorghum. An increase in LAI with increasing population density is associated with effective light interception (Tollenaar, Aguilera & Nissanka, 1997) and may thus allow high plant densities to attain greater photosynthetic output per unit area and greater biomass production (Sangoi *et al*., 2002). Williams *et al*. (1968), as cited by Tetio-Kagho & Gardner (1988), reported a direct relationship between LAI and light interception and resulting photosynthesis.

The main effect of N fertility was significant for LAI at anthesis (63 DAE at Sirinka and 69 DAE Kobo). Nitrogen fertilization increased LAI by up to 27% at Sirinka and by 16% at Kobo (data not shown). The increase in LAI with N supply could be due to the effect of N on the rate of leaf expansion (Muchow, 1988) and reduced rate of leaf senescence (Van Keulen, Goudriaan & Seligman, 1989). The effect of the nitrogen x population density interaction effects on LAI was not large. Significant differences were observed only at 42 DAE at Sirinka and 69 DAE at Kobo where population densities of 166 666 and 88 888 plants ha^{-1} under both fertilized and unfertilized conditions provided higher LAIs (data not shown).

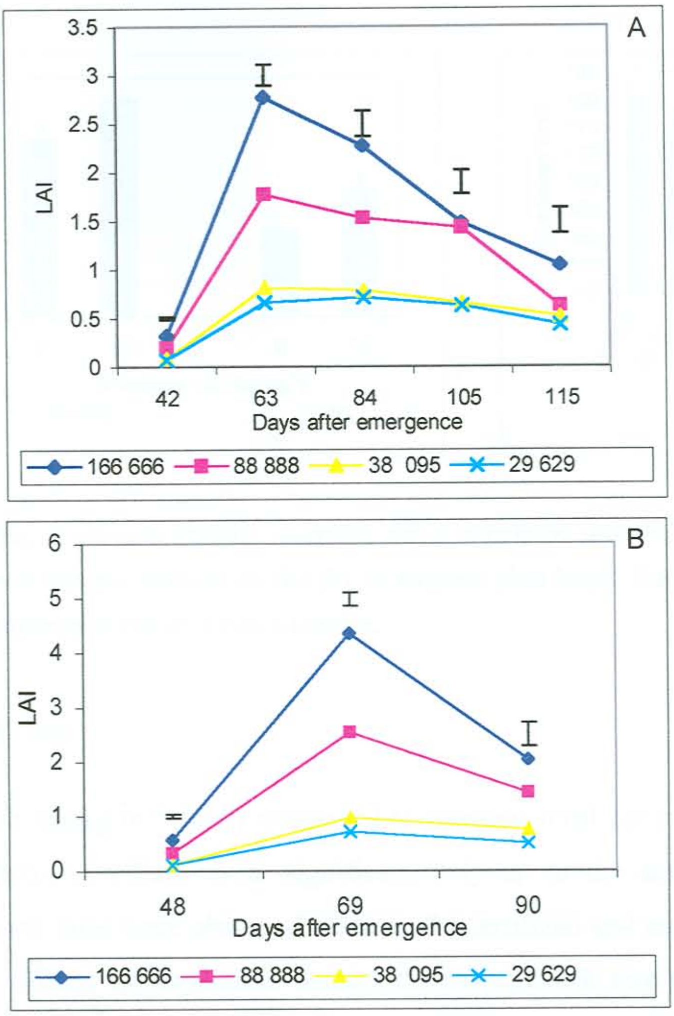
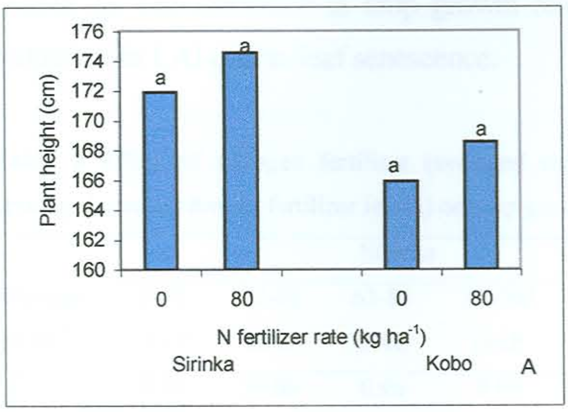


Figure 1 Effect of population density (averaged across nitrogen fertilizer levels) on leaf area index (LAI) at Sirinka (A) and Kobo (B). Vertical lines on each period of measurement indicate LSD values at $P \leq 0.05$.

Plant height

Nitrogen fertilization resulted in somewhat taller plants at both sites, but differences were not statistically significant (Figure 2A). Significant differences in plant height were observed only between the main effects of population density at both sites (Figure 2B), probably as a result of competition for light. The 166 666 population resulted in taller plants than the two lower plant densities at both sites. Although plants at the higher density were approximately 10% taller no clear effect on stem lodging was observed. Similar results were reported in sorghum by Blum (1970) and Martin & Kelleher (1984).



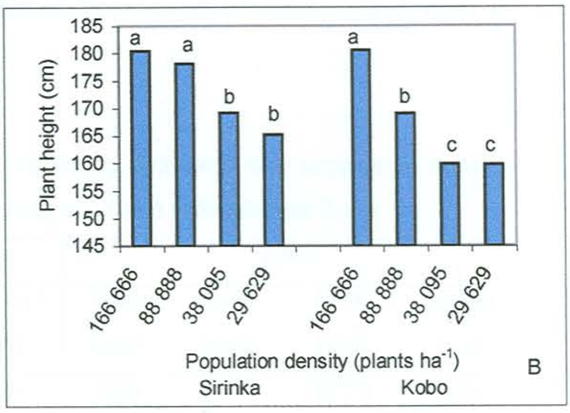


Figure 2 Effect of nitrogen fertilizer (averaged across population densities) (A) and population density (averaged across nitrogen fertilizer levels) (B) on sorghum plant height. Bars with the same letter are not significantly different at P≤0.05 for each location.

Crop growth rate

Crop growth rate (g m^{-2} day^{-1}) responded to nitrogen fertilizer treatments only at Sirinka. Nitrogen fertilizer effects were significant only up to the anthesis stage, after which similar growth rates were observed between the fertilized and unfertilized plots (Table 2). Significant effects of population density on crop growth rate were observed up to the anthesis stage at Sirinka. However, at Kobo it extended up to 90 DAE. Crop growth rate increased with the increase in population density. The highest density (166 666 plants ha^{-1}) had a significantly higher crop growth rate (Table 2). Differences in crop growth rate between densities in the early growth stages could be attributed to larger LAI and its influence on the amount of radiation intercepted. This is indicated by the close and positive relationship between crop growth rate and LAI (r^2 between 0.97* and 0.99** at Sirinka and r^2 between 0.96* and 0.99** at Kobo). Leaves in the high density treatments were narrow and less droopy and the plants themselves were taller. It has been reported that such features of the canopy are more favourable to light penetration per unit leaf area (Fischer & Wilson, 1975). Similarly, Van Averbeke & Marais (1992) reported that a higher LAI, obtained by increasing the planting density, resulted in a higher CGR in maize. Crop growth rates for all densities increased to a maximum around anthesis (42-63

DAE at Sirinka and 48-69 DAE at Kobo) and then declined during the grain filling period (Table 2). The reduction in crop growth rate after anthesis could be associated with a reduction in LAI due to leaf senescence.

Table 2 Effect of nitrogen fertilizer (averaged across population densities) and population density (averaged across nitrogen fertilizer levels) on crop growth rate (g m^{-2} day^{-1}) at Sirinka and Kobo

	Sirinka					Kobo			
Nitrogen (kg ha^{-1})	0-42 DAE	42-63 DAE	63-84 DAE	84-105 DAE	105-115 DAE	0-48 DAE	48-69 DAE	69-90 DAE	90-101 DAE
0	1.9b	30.6b	0.9a	8.9a	0.4a	3.8a	21.4a	11.3a	6.9a
80	2.5a	37.0a	4.0a	6.8a	4.6a	4.4a	22.6a	12.5a	18.9a
Population density (plants ha^{-1})									
166 666	4.0a	63.4a	-2.6a	10.01a	10.8a	8.3a	39.7a	20.1a	7.7a
88 888	2.7b	36.4b	5.3a	9.16a	-3.5a	4.8b	25.1b	14.1ab	14.5a
38 095	1.1c	20.8c	4.0a	5.81a	3.5a	1.9c	13.2c	6.4b	20.6a
29 629	1.1c	14.5c	3.3a	6.33a	-1.0a	1.4c	10.0c	7.1b	8.9a

DAE = days after emergence. Means within columns for each comparison followed by the same letters are not significantly different at $P \leq 0.05$.

Leaf, stem, panicle and total dry mass production

Leaf, stem, panicle and total dry mass production responded to nitrogen fertilizer and population density treatments. However, the responses of each parameter differed for each period of measurement and for each location. Leaf dry mass differed consistently between the main effects of nitrogen fertilizer (Table 3) and population density (Figure 3A & D), except the nitrogen effect at 105 DAE at Sirinka and 48 DAE at Kobo. Nitrogen application increased leaf dry mass by 16 to 25% at Sirinka and 23 to 30% at Kobo (Table 3). Leaf dry mass also increased with increasing population density at both locations (Figure 3A & D). The only significant differences observed between the interaction effects on leaf dry mass were at 42 DAE at Sirinka, where the highest population density, in combination with 80 kg N ha^{-1}, gave the highest leaf dry mass (Table 4).

The main effects of nitrogen fertilizer on stem dry mass were significant throughout the growth stage at Sirinka and only at 48 DAE at Kobo (Table 3). Nitrogen fertilization increased stem dry mass by up to 20 to 36% at Sirinka and 29% at Kobo. Stem dry mass increased significantly following the increase in population density (Figure 3 B & E). The nitrogen x population density interaction effects on stem dry mass were significant only at 42 DAE at Sirinka and at 48 and 90 DAE at Kobo (Table 4). Stem dry mass tended to increase with nitrogen fertilization in all densities. Statistically significant differences, however, were observed between the unfertilized and fertilized plots of the highest density (166 666 plants ha^{-1}) (Table 4).

Leaf and stem dry mass accumulation increased linearly with time until anthesis and decreased markedly during grain filling (Figure 3). Part of the loss in stem and leaf dry mass after anthesis represents mobilization of labile food reserves to the seeds (Papakosta & Gagianas, 1991).

Nitrogen fertilizer increased panicle dry mass per unit area at all measurement periods at Sirinka, but only at 101 DAE at Kobo (Table 3). Panicle dry mass was increased with nitrogen fertilization by up to 49% at Sirinka and 28% at Kobo. Panicle dry mass per unit area increased with increasing population density (Figure 3 C & F). The nitrogen x population density interaction effect was very infrequent with significant effects only being observed at 115 DAE at Sirinka (Table 4). Panicle dry mass tended to increase with nitrogen fertilization, however, statistically significant differences were observed between the unfertilized and fertilized plots of the highest density (166 666 plants ha^{-1}).

Table 3 Effect of nitrogen fertilizer (averaged across population densities) on leaf, stem, panicle and total dry mass (g m^{-2}) in sorghum

	Nitrogen	Sirinka					Kobo			
	(kg ha^{-1})	42 DAE	63 DAE	84 DAE	105 DAE	115 DAE	48 DAE	69 DAE	90 DAE	101 DAE
Leaf	0	46.1b	118.5b	78.9b	82.2a	80.0b	96.7a	118.2b	102.5b	92.6b
	80	56.8a	137.9a	98.5a	94.6a	97.0a	104.8a	144.9a	133.2a	114.3a
Stem	0	35.1b	304.8b	318.8b	281.3b	285.5a	83.5b	400.2a	357.0a	294.5a
	80	47.6a	388.4a	403.7a	338.3a	323.5a	108.0a	416.9a	340.7a	328.9a
Panicle	0	-	116.7b	161.9b	382.4b	383.7b	-	113.1a	410.7a	559.9b
	80	-	133.2a	242.0a	454.6a	512.7a	-	126.1a	477.6a	716.5a
Total	0	81.3b	540.2b	559.7b	745.9b	749.3b	180.2a	631.6a	870.3a	947.0b
	80	104.5a	659.5a	744.3a	887.6a	933.3a	212.9a	687.9a	951.5a	1159.8a

DAE = Days after emergence. Means within columns followed by the same letter for each parameter are not significantly different at $P \leq 0.05$.

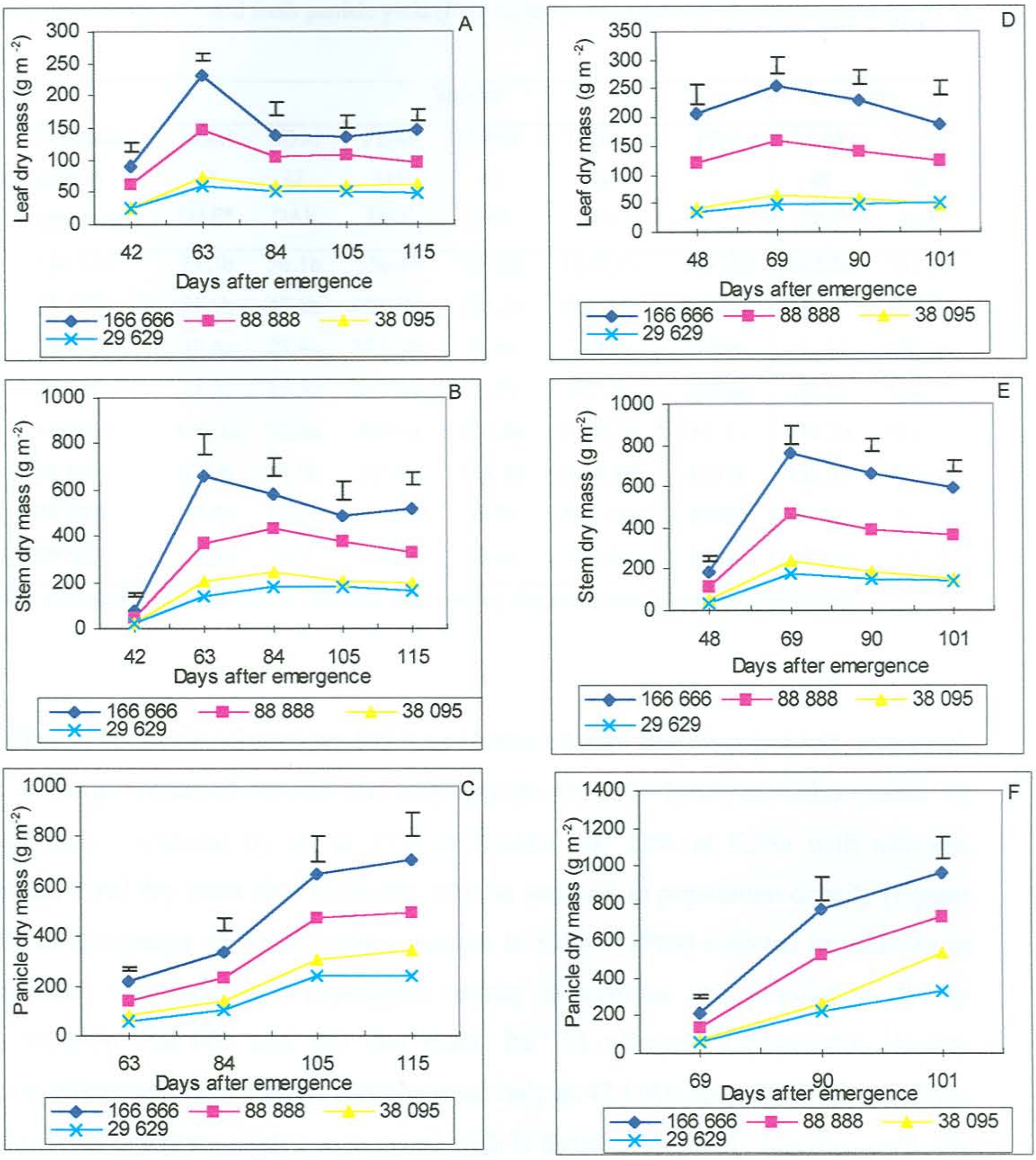


Figure 3 Effect of population density (averaged across nitrogen fertilizer levels) on leaf, stem and panicle dry mass at Sirinka (A-C) and Kobo (D-F). Vertical lines on each period of measurement indicate LSD values at P ≤0.05.

Table 4 Effect of nitrogen fertilizer x population density on leaf (LDM), stem (SDM), panicle (PDM) and total (TDM) dry mass (g m^{-2}) and fresh panicle yield (FPY kg ha^{-1}) at Sirinka and on stem dry mass (g m^{-2}) at Kobo

		Sirinka						Kobo	
Nitrogen (kg ha^{-1})	Population density (plants ha^{-1})	LDM 42 DAE*	SDM 42 DAE	PDM 115 DAE	TDM 42 DAE	TDM 115 DAE	FPY	SDM 48 DAE	SDM 90 DAE
0	166 666	73.3b	56.1b	556.1b	129.4b	1168.3b	3437bc	162.2b	763.3a
	88 888	59.5b	45.6b	428.1bc	105.2b	826.7cd	3437bc	90.4c	339.5d
	38 095	30.6c	23.4c	283.8de	53.9c	537.2e	2969c	54.3d	170.6e
	29 629	21.2c	15.5c	267.1de	36.7c	465.2e	2888c	27.2d	154.7e
80	166 666	108.3a	95.6a	865.6a	203.9a	1593.9a	5511a	217.2a	561.1b
	88 888	67.0b	51.9b	565.6b	118.8b	1024.3bc	4237b	132.1b	440.6c
	38 095	22.4c	16.4c	399.0cd	38.7c	663.7de	2993c	44.6d	207.1e
	29 629	29.8c	26.7c	220.7e	56.6c	451.3e	2933c	38.4d	154.2e

* Days after emergence. Means within columns followed by the same letters are not significantly different at P≤0.05.

The main effects of nitrogen fertilizer increased total dry mass per unit area at all periods of measurement at Sirinka and only at maturity (101 DAE) at Kobo (Table 3). Total dry mass increased by up to 33% at Sirinka and 22% at Kobo with nitrogen fertilization. Total dry mass also increased with an increase in population density (Figure 4A & B). In agreement with this finding, Amano & Salaza (1989) reported an increase in total dry mass with increasing population density in sorghum at a population density ranging between 100 000 and 300 000 plants ha^{-1}. A nitrogen x population density interaction effect on total dry mass was observed only at 42 DAE and 115 DAE at Sirinka (Table 4). Total dry mass tended to increase with N fertilization in all densities, with the exception of the lowest density (29 629 plants ha^{-1}). Statistically significant differences, however, were observed only between the fertilized and unfertilized plots of the highest population density (166 666 plants ha^{-1}).

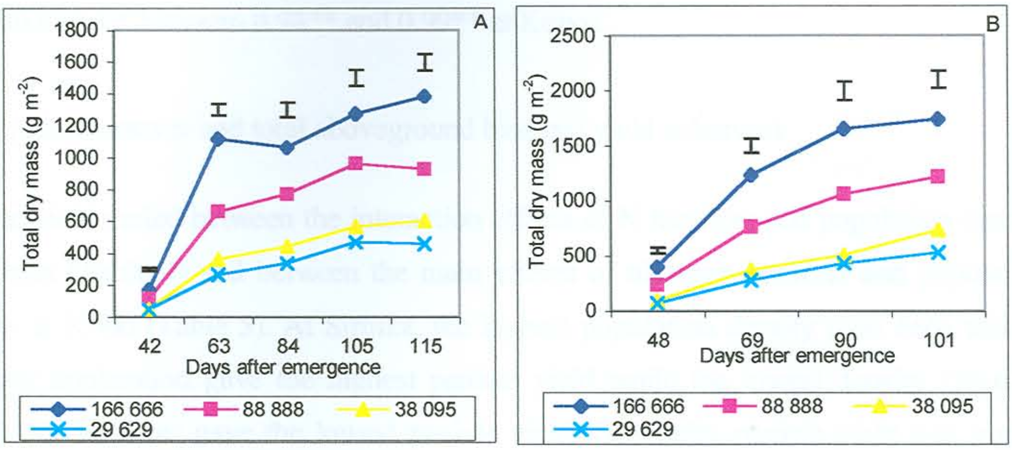


Figure 4 Effect of population density (averaged across nitrogen fertilizer levels) on total dry mass at Sirinka (A) and Kobo (B). Vertical lines on each period of measurement indicate LSD values at P ≤0.05.

The higher leaf, stem and total dry mass with N fertilization could be due to the positive effect of N on canopy development as a result of alterations in leaf area development. Plants receiving N fertilization might have larger leaf area index which can have an effect on radiation interception and thus on photosynthetic activity of the canopy (Lugg & Sinclair, 1981 as cited by Muchow, 1988). Muchow & Davis (1988) also ascribed increased dry mass accumulation in sorghum and maize in response to N fertilization to higher radiation interception and radiation use efficiency.

Several researchers have reported increases in leaf, stem, panicle and total dry mass production with increasing plant density. Saiieb, Singh & Singh (1997) reported increased leaf, stem and total dry mass for sorghum with increasing density (80 000 to 120 000 plants ha^{-1}). Martin & Kelleher (1984) also reported increased leaf, stem and total dry mass production in sorghum as population density was increased from 80 000 to 160 000 plants ha^{-1}. Muchow & Davis (1988) reported that dry mass production was dependent on the interception of incident radiation by the crop canopy and the efficiency with which it is used to produce dry mass. Thus, the higher LAI of the highest plant density, indicative of much greater absorption of photosynthetically active radiation could be the reason for the higher dry mass (leaf, stem, panicle and total) production in the highest population density. This justification can be supported by the highly positive relationship between, for instance, total dry mass and LAI (r^2 between 0.89** and 0.99** at Sirinka and r^2 between 0.98** and 0.99** at Kobo).

Fresh panicle, stover and total aboveground biomass yield at harvest

Panicle yield varied between the interaction effects of N fertilizer and population density at Sirinka (Table 4) and between the main effects of nitrogen fertilizer and population density at Kobo (Table 5). At Sirinka, the highest population density (166 666) with N fertilizer application gave the highest panicle yield while the lowest density (29 629) without N fertilizer gave the lowest panicle yield. Generally, panicle yield was higher with N fertilizer application. At Kobo, nitrogen fertilization increased panicle yield by 28%. Averaged across nitrogen fertilizer treatments, panicle yield increased in linear response to increasing population density. Stover and total aboveground biomass yields increased by more than 30% with nitrogen fertilization at Sirinka (Table 5). At both sites, stover and total aboveground biomass yields increased linearly with increasing population density (Table 5).

Table 5 Effect of nitrogen fertilizer and population density on fresh panicle yield (FPY kg ha^{-1}), stover yield (SY kg ha^{-1}) and total aboveground biomass yield (TBY kg ha^{-1}) at Sirinka and Kobo

Nitrogen	Sirinka		Kobo		
(kg ha^{-1})	SY	TBY	FPY	SY	TBY
0	4127b	6816b	2993b	4104a	7722a
80	5444a	8910a	3822a	4052a	7999a
Population density (plants ha^{-1})					
166 666	5983a	9800a	4637a	5408a	9812a
88 888	5172ab	8449a	3941b	4498b	8606a
38 095	4307bc	7020b	2682c	3526c	6894b
29 629	3680c	6184b	2370c	2880c	6128b
Contrasts§					
Linear	**	**	**	**	**
Quadratic	NS	NS	NS	NS	NS

Means within columns for each comparison followed by the same letters are not significantly different at P<0.05. §Contrasts are for population density. ** Significant at P≤0.01. NS = non-significant difference.

Grain yield and yield components

Grain yield responded to the interaction effects of nitrogen fertilizer and population density at Sirinka (Table 6). Grain yield tended to increase in all population densities with nitrogen fertilization. However significant differences were observed only between the fertilized and unfertilised plots of the two highest densities (166 666 and 88 888 plants ha^{-1}). Under no fertilized condition grain yield did not differ between the population density treatments, but with the application of 80 kg N ha^{-1} the two highest population densities gave significantly higher grain yields. At Kobo, grain yield responded only to the main effect of population density (Table 6). Averaged over nitrogen fertilizer treatments, grain yield increased in linear response to increasing population density. Grain yield with the highest density (166 666 plants ha^{-1}) was greater by 35% over the lowest population density (29 629 plants ha^{-1}) and by 7% over the conventionally recommended population density (88 888 plants ha^{-1}).

Table 6 Effect of nitrogen fertilizer and population density on sorghum grain yield (kg ha^{-1}) at Sirinka and Kobo

	Nitrogen	Population density (plants ha^{-1})				
Location	(kg ha^{-1})	166 666	88 888	38 095	29 629	Mean
Sirinka	0	2967c	2735c	2690c	2366c	2689B
	80	4667a	3818b	2737c	2642c	3466A
	Mean	3817A	3277AB	2714BC	2504C	
Kobo	0	4493a	3479a	3210a	3288a	3617A
	80	4315a	4739a	3526a	3209a	3947A
	Mean	4404A	4109AB	3368BC	3248C	
	Contrasts§	Sirinka	Kobo			
	Linear	**	**			
	Quadratic	NS	NS			

Means within columns and rows followed by the same lowercase letters; means within rows followed by the same uppercase letters; and means within columns followed by the same uppercase letters are not significantly different at P≤0.05. § Contrasts are for population density. ** Significant at P<0.01. NS = non-significant difference.

Grain yield, averaged across N fertilizer treatments, was negatively correlated to yield components (Table 7). However, it was positively correlated to head and seed number per unit area (Table 7). This correlation emphasizes that under high population densities, the yield components will be reduced possibly owing to competition for resources between plants. However, the higher number of heads per hectare compensated for the reduction in grain yield per plant due to reduction in yield components. The higher head and seed number per unit area were the major yield components contributing (r^2 = 0.97** and 0.99** at Sirinka and 0.92* and 0.95* at Kobo) to the yield increase under high population densities.

Variation in grain yields due to population density, were associated with variation in LAI (r^2 between 0.91** and 0.99** at Sirinka and between 0.92* and 0.97* at Kobo), which would affect the photosynthetic activity of the canopy (Cox, 1996). Similarly, variation in grain yield due to population density was related to variation in total dry mass production (r^2 between 97** and 0.99** at Sirinka and r^2 between 0.94* and 0.95* at Kobo) and crop growth rate (r^2 between 0.89* and 0.97** at Sirinka and r^2 between 0.94* and 0.95* at Kobo). Fischer & Wilson (1975) reported increased yields from high plant population densities in sorghum despite the reduced yield per individual plant. M'Khaitir & Vanderlip (1992) also observed increased sorghum grain yield following an increase in planting densities ranging between 15 000 to 135 000 plants ha^{-1}. Amano & Salazar (1989) reported yield increases of 9 and 21% as sorghum plant densities were increased from 100 000 to 200 000 and 300 000 plants ha^{-1}, respectively. Grimes & Musick (1960), as cited by Amano & Salazar (1989), indicated that sorghum is tolerant to varying plant population densities due to its ability to tiller and produce larger heads at low plant density and smaller heads at high density.

Table 7 Simple correlation coefficients between grain yield and yield components (averaged across N fertilizer treatments, n=4)

Yield components	Sirinka	Kobo
Panicle length (cm)	r = -0.99**	r = -0.98**
Panicle weight plant^{-1}	r = -0.99**	r = -0.98**
Seed weight panicle^{-1}	r = -0.99**	r = -0.97*
Seed number panicle^{-1}	r = -0.99**	r = -0.93NS
1000-seed weight (g)	r = -0.96*	r = -0.88NS
Head number m^{-2}	r = 0.98**	r = 0.96*
Seed number m^{-2}	r = 0.99**	r = 0.97*

*, ** denote significance at 0.05 and 0.01 probability level. NS = non-significant difference.

Yield components such as panicle length (PL), panicle weight plant^{-1} (PWP), seed weight panicle^{-1} (SWP), seed number panicle^{-1} (SNP) and 1000-seed weight (TKW) were affected by the main effects of nitrogen fertilizer and population density (Tables 8 and 9). Averaged over population density treatments, PL, PWP, SWP and SNP responded to nitrogen fertilization at both locations, except for PL and PWP at Kobo. TKW responded negatively to nitrogen fertilization at Sirinka (Table 8) and did not respond at Kobo (Table 9). Similar results were reported by Ogunlela & Okoh (1989).

Averaged over nitrogen fertilizer treatments, PL, PWP, SNP and TKW increased in linear response to decreasing population densities, while SWP had a quadratic response. The negative relationship between yield components and population density could be due to reduced competition for resources under low densities and thus better growth of individual plants. Increasing population density to 166 666 plants ha^{-1} reduced PL by 21 and 7%, PWP by 50 and 23%, SWP by 50 and 23% and SNP by 39 and 22% compared to the lowest (29 629 plants ha^{-1}) and conventional (88 888 plants ha^{-1}) densities at Sirinka (Table 8). The corresponding values at Kobo were 16 and 5% for PL, 46 and 25% for PWP, 47 and 25% for SWP and 35 and 19% for SNP (Table 9). These observations are in accordance with the results of several workers (Ogunlela & Okoh, 1989; M'Khaitir & Vanderlip, 1992; Berenguer & Faci, 2001). Goldsworthy & Tayler (1970) as cited by Ogunlela & Okoh (1989) indicated that differences in seed number might be due to variations in the number of flower initials formed, or to variations in the number which survive to produce grain.

The observed increase in yield components, with a decrease in population density, indicates the capacity of sorghum to adjust yield components through compensatory growth. Nevertheless, the yield compensatory mechanisms observed at lower densities were not capable of equilibrating grain yield to that obtained from the highest density. This is due to the fact that the significantly lower number of panicles per unit area offset yield compensation advantages in the lower population densities. This indicates that although considerable reductions occurred in yield components in densely populated crops, it is the number of heads that actually contribute to higher yield in closely planted sorghum (Kudasomannavar *et al*., 1980). This observation leads to the conclusion that data on growth and yield per plant may not be a satisfactory parameter for describing and `understanding the response of sorghum to population density.

Table 8 Effect of nitrogen fertilizer (averaged across population densities) and population density (averaged across nitrogen fertilizer levels) on yield components of sorghum at Sirinka

Nitrogen (kg ha^{-1})	Panicle length (cm)	Panicle weight (g panicle^{-1})	Seed weight (g panicle^{-1})	Seed number panicle^{-1}	1000-seed weight (g)	Head number m^{-2}	Seed number m^{-2}
0	24.7b	63.3b	51.6b	1966b	28.8a	7a	13860b
80	26.4a	78.1a	64.0a	2243a	26.7b	7a	15904a
Population density (plants ha^{-1})							
166 666	22.4c	46.5b	38.1b	1530c	25.1b	13a	25496a
88 888	24.2b	60.2b	49.2b	1953b	25.9b	8b	17360b
38 095	27.4a	82.5a	67.1a	2420a	29.3a	4c	9221c
29 629	28.4a	93.5a	76.7a	2515a	30.7a	3c	7451c
Contrasts§							
Linear	**	**	**	**	**	**	**
Quadratic	NS	NS	*	NS	NS	**	**

Means within columns for each comparison followed by the same letters are not significantly different at P≤0.05. § Contrasts are for population density. *, ** Significant at the 0.05 and 0.01 probability level, respectively. NS denotes non-significant difference.

Table 9 Effect of nitrogen fertilizer (averaged across population densities) and population density (averaged across nitrogen fertilizer levels) on yield components of sorghum at Kobo

Nitrogen ($kg\ ha^{-1}$)	Panicle length (cm)	Panicle weight ($g\ panicle^{-1}$)	Seed weight ($g\ panicle^{-1}$)	Seed number $panicle^{-1}$	1000-seed weight (g)	Head number m^{-2}	Seed number m^{-2}
0	26.7a	81.1a	68.9b	2632b	27.8a	6b	19344a
80	26.9a	91.8a	82.9a	3049a	25.8a	7a	22144a
Population density ($plants\ ha^{-1}$)							
166 666	24.5d	58.4b	48.6c	2233c	23.2c	12a	37212a
88 888	25.7c	78.0b	64.8b	2733b	25.8bc	8b	24294b
38 095	27.9b	101.5a	98.7a	2978ab	30.4a	4c	11344c
29 629	29.1a	107.9a	91.6a	3417a	27.7ab	4c	10124c
Contrasts§							
Linear	**	**	**	**	**	**	**
Quadratic	NS	NS	**	NS	NS	**	**

Means within columns for each comparison followed by the same letters are not significantly different at $P \leq 0.05$. § Contrasts are for population density. *, ** Significant at the 0.05 and 0.01 probability level, respectively. NS denotes non-significant difference.

Nitrogen uptake and concentration

Nitrogen fertilization increased stover N uptake by 51%, grain N uptake by 36%, total N uptake by 41% and stover N concentration by 17% at Sirinka (Table 10). Grain N concentration did not, however, respond to N fertilizer treatments at Sirinka. At Kobo, N fertilization markedly increased stover N uptake by 35%, total aboveground biomass N uptake by 14% and stover N concentration by 41% (Table 10). Grain N uptake and concentration did not, however, respond to N fertilizer treatments at Kobo. Significant differences in N uptake (stover, grain and total plant) between population density treatments were not observed at Sirinka. However, at Kobo population density significantly affected stover, grain and total aboveground biomass N uptake where these parameters increased with an increase in population density (Table 10). The higher N uptake at the higher densities could be due to a greater number of plants per unit area resulting in higher stover, grain and total dry matter production. This observation is in accordance with the results of Kudasomannavar *et al*. (1980).

Stover and grain N concentrations at Sirinka differed between population density treatments where the values of both parameters increased with a decrease in population density (Table 10). The lower stover and grain N concentrations in the higher densities could be due to greater competition between plants for soil N. Similar results were reported by Rosolem *et al.* (1993) who found reduced stover and grain N concentrations as sorghum population density increased. At Kobo, grain N concentration did not respond to population density while stover N concentration did not follow any trend (Table 10).

Nitrogen harvest index and nitrogen use efficiency

The effects of both nitrogen fertilizer and population density treatments on nitrogen harvest index (the proportion of absorbed N that is distributed to grain) were not great, but tended to increase with an increase in population density at Sirinka (Table 10).

Nitrogen use efficiency (utilization of absorbed N for grain production) was significantly affected by the main effects of nitrogen fertilizer and population density treatments only at Sirinka (Table 10). Nitrogen use efficiency was higher in plants which did not receive nitrogen fertilization. Nitrogen use efficiency increased following the increase in population density where about 53 kg grain by the highest density and 39 kg grain by the lowest density were produced for each kg of N taken up.

Grain protein concentration and protein yield

Grain protein concentration did not respond to nitrogen fertilizer treatment at Sirinka and to neither nitrogen nor population density treatments at Kobo (Table 10). However, at Sirinka grain protein concentration differed between population density treatments where grain protein concentration tend to increase as population density decreased (Table 10). Similar results were reported by Kudasomannavar *et al.* (1980) and Ogunlela & Okoh (1989). Grain protein yield responded to nitrogen fertilizer at Sirinka and to population density at Kobo (Table 10). Grain protein yield increased by 37% with nitrogen fertilization at Sirinka, while at Kobo it was found to respond to increasing population density but not to nitrogen fertilization. Ogunlela & Okoh (1989) also reported 52% increase in sorghum grain protein yield with the application of 60 kg N ha^{-1}.

Table 10 Effect of nitrogen fertilizer (averaged across population densities) and population density (averaged across nitrogen fertilizer levels) on nitrogen use efficiency attributes at Sirinka and Kobo

Location	Nitrogen ($kg\ ha^{-1}$)	SNU ($kg\ ha^{-1}$)	GNU ($kg\ ha^{-1}$)	TNU ($kg\ ha^{-1}$)	SNC (%)	GNC (%)	NHI	NUE ($kg\ kg^{-1}$)	GPC (%)	GPY ($kg\ ha^{-1}$)
Sirinka	0	19b	41b	60b	0.47b	1.53a	0.68a	46a	9.6a	257b
	80	29a	56a	85a	0.55a	1.63a	0.66a	41b	10.2a	351a
	Population density (plants ha^{-1})									
	166 666	22a	54a	76a	0.36c	1.38c	0.71a	53a	8.6c	337a
	88 888	25a	50a	74a	0.48b	1.49bc	0.66b	45b	9.3bc	310a
	38 095	25a	50a	75a	0.58a	1.83a	0.67b	36c	11.5a	310a
	29 629	24a	42a	65a	0.64a	1.64b	0.64b	39c	10.3b	259a
Kobo	0	12.0b	72.0a	84.0b	0.29b	2.01a	0.86a	43.0a	12.5a	450.1a
	80	16.2a	79.2a	95.4a	0.41a	2.00a	0.83a	41.9a	12.5a	495.0a
	Population density (plants ha^{-1})									
	166 666	18.8a	88.8a	107.6a	0.35ab	2.03a	0.83a	41.2a	12.7a	555.2a
	88 888	12.4b	83.47a	95.9a	0.28b	2.03a	0.87a	43.0a	12.7a	521.7a
	38 095	15.4ab	65.0b	80.4b	0.44a	1.94a	0.82a	42.3a	12.1a	406.4b
	29 629	9.8b	65.1b	74.9b	0.35ab	2.02a	0.87a	43.4a	12.6a	406.9b

SNU, GNU, TNU, SNC, GNC, NHI, GPC, GPY, and NUE represent stover N uptake, grain N uptake, total plant N uptake, stover N concentration, grain N concentration, N harvest index, grain nitrogen use efficiency, grain protein concentration and grain protein yield. Means within columns for each comparison followed by the same letters are not significantly different at $P \leq 0.05$.

Conclusion

Increasing plant density resulted in increased growth and yield of sorghum on a per unit area basis. Grain, stover and total aboveground biomass yields were generally greater for the higher plant densities. However, plant growth, yield and yield components on individual plant basis increased with decreasing density. Grain yield per plant at high population densities was lower owing to lower seed number and lower seed weight per panicle, smaller head size and lower 1000-seed weight. This indicates that important yield compensation processes have occurred as the population density declined. The observed yield compensation mechanisms could not, however, equilibrate the final yield as the yield compensation advantages were offset by the lower head and seed number per square meter.

Results indicated that differential CGR, TDM production and LAI per unit area were the major growth dynamic mechanisms responsible for yield differences across densities. Results also indicated that an increase in population density should be accompanied by the elimination of nitrogen stress, which slowed down leaf area development, dry mass production and crop growth rate, especially at Sirinka. Generally, under the present climatic conditions and the cultivar used, the conventional planting density (88 888 plant ha^{-1}) being used in NE Ethiopia is not the optimum density as increases in grain yield were found to be linear up to a population density of 166 666 plants ha^{-1}. These results also showed the ability of the newly released cultivar ICSV 111 to tolerate population stress as shown by its linear response in most parameters to increasing planting density. Increasing plant population was also associated with increased stover yield, which is an important consideration for small-scale farmers to whom stover has multiple uses.

Generally, sorghum yield-density relationships exhibited an asymptotic relationship in the present study, a relationship in which yield approaches a maximum as plant density increases and it is impossible to determine an optimum density. Thus, it can be recommended that further study should be conducted to determine the optimum planting density. Willey & Heath (1969) as cited by Shirtliffe & Johnston (2002) indicated that yield-density relationships in plants generally follow either an asymptotic or a parabolic pattern. A hyperbolic yield-density relationship occurs when there is a yield maximum at an optimum plant density and yield decreases at higher densities.

Farmland is a scarce resource in NE Ethiopia where the average land holding is approximately 0.1 ha per family. The results of this study, which revealed increasing productivity through increasing plant population, would be most welcome to the small-scale farmers to whom increasing productivity through increasing farm size is not possible.

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