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Influence of nitrogen fertilization on water relations, photosynthesis, carbohydrate and nitrogen metabolism of diverse pearl millet genotypes under arid conditions

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SUMMARY

Effects of nitrogen fertilization (80 kg N/ha) were studied on pearl millet (*Pennisetum glaucum*) genotypes including hybrids (MH-179 and HHB-67), composites (CZ-IC-923 and CZP-9604) and land races (Barmer population and CZ-IC-718) grown for 2 consecutive years (1997 and 1998) under rainfed conditions of the Indian arid zone. Nitrogen application significantly increased the grain and stover yields in all the genotypes, particularly in the hybrids during both the years but more so in 1997, characterized by late onset of rains followed by adequate precipitation (299·5 mm). Notwithstanding lower plant water potential and leaf relative water content, N fertilized plants displayed significantly higher photosynthetic rates, leaf area, levels of total chlorophyll, starch, reducing sugars, soluble protein and free amino acids and nitrate reductase activity as compared with unfertilized control plants in all the genotypes during both the years.

Genotypes HHB-67 and Barmer population during 1997 and HHB-67 and CZ-IC-718 during 1998 provided significantly higher grain yields than other genotypes whereas dry matter production was highest in cv. Barmer population during both the years. These genotypes generally maintained higher rates of photosynthesis, more efficient carbohydrate metabolism and higher nitrate reductase activity leading to better performance. Relatively higher yields of land races than composites and comparable with those of hybrids indicated adaptation of these cultivars to arid conditions and maintenance of several characteristics for their superior performance which could be further augmented by N application.

Fertility induced improvement of metabolic efficiency, coupled with higher photosynthesis and nitrate reductase activity for efficient N utilization seem to be the control mechanisms, for enhanced growth and yield of diverse pearl millet genotypes under limited water conditions.

INTRODUCTION

In drought-prone arid and semi-arid parts of western Rajasthan in India, pearl millet is grown extensively under rainfed conditions. Yields, however, are very low principally due to recurring droughts and little or no soil fertilization (Harinarayana 1987). The crop is known to respond favourably to fertilizers, irrigation and improved management conditions (Kathju *et al.* 1993; Bhatnagar *et al.* 1998). Of the three macronutrients, response to N has almost been universal in all the regions of the country where pearl millet is grown. The optimum rate of N fertilization in experiments averaged over 5 years and 30 locations ranged from 92 to 137 kg/ha at response level of 6·0 to 10·5 kg grain per kg N applied (De & Gautam 1987). Joshi (1984) reported considerable variation in N optima between years and among pearl millet genotypes due to variations in quantum and distribution pattern of rainfall under arid conditions. In this regard merit of adequate soil fertility in alleviation of adverse effects of droughts on growth and yield of several crops including pearl millet is well documented (Lahiri 1980; Garg *et al.* 1984; Kathju *et al.* 1993). Application of N is known to reduce effects of field droughts on pearl millet through changes in plant water relations and leaf metabolism (Garg *et al.* 1993; Kathju *et al.* 1993). However, genotypic differences to N fertilization under such situations have received less attention in relation to plant water relation parameters, and physiological and biochemical pro-

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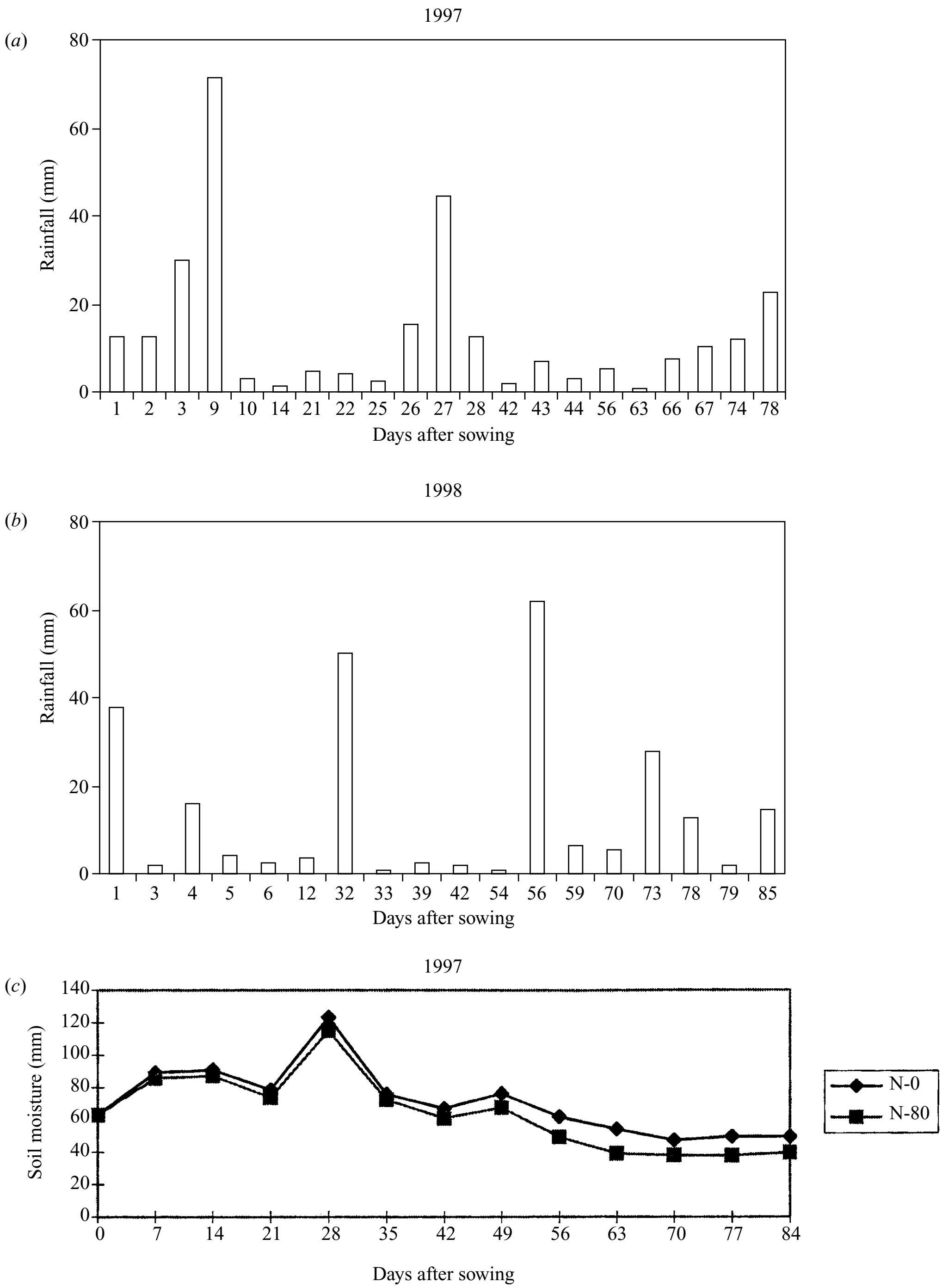

Fig. 1. For legend see opposite.

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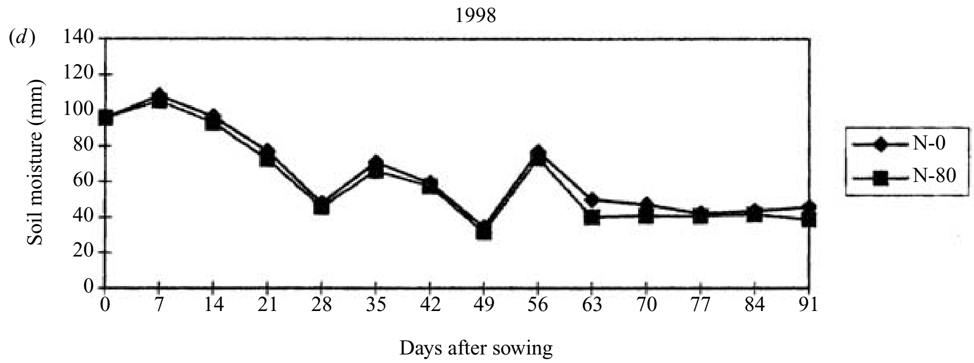

Fig. 1. Comparative rainfall pattern and soil moisture up to one metre depth in 1997 and 1998 in plots maintaining pearl millet genotypes grown with (N-80) and without (N-0) nitrogen application. The lines indicate the lowest level (45 mm) of soil moisture available to crop.

cesses. The present paper relates some findings in this area.

MATERIALS AND METHODS

The present investigation was conducted for 2 consecutive years, 1997 and 1998, with six pearl millet (*Pennisetum glaucum* (L.) R.Br. emend Stuntz) genotypes including hybrids (MH-179 and HHB-67), composites (CZ-IC-923 and CZP-9604) and landraces (Barmer population and CZ-IC-718). The crops were grown at 45 × 15 cm spacings in field plots (4·5 × 3·6 m) on loamy sand soil at the Central Research Farm of this Institute at Jodhpur. The soil was a Typic Camborthids (7·1 % clay, 5·6 % silt, 63·1 % fine sand and 24·1 % coarse sand) having 0·28 % organic carbon and 0·023 % total nitrogen. The soil contained 80 kg/ha available N, 12 kg/ha available P and 120 kg/ha available K. Plants were grown either without fertilizer nitrogen (low fertility – LF) or with 80 kg N/ha (improved fertility – IF) applied as urea at sowing. A basal dose of 17·5 kg P/ha and 16·6 kg K/ha was given in all the plots at the time of sowing. A factorial completely randomized design was adopted with genotypes and nitrogen as two factors with four replications. Due to late onset of monsoon in 1997 the crop was sown on 30 July, but on 1 July in 1998.

The consumption of moisture was determined through water balance studies. The soil moisture was determined gravimetrically up to 1·0 m depth at weekly intervals from sowing to harvest. Observations were recorded on plant water potential (ψ_{plant}) using a Pressure Chamber (PMS Instrument Company, USA) and relative water content (RWC) adopting a standard procedure (Slatyer & McIlroy 1961) at panicle initiation (30 DAS) and flowering (50 DAS) stages during both the years. Leaf area (LICOR-3000 Area Meter) and net photosynthesis (LICOR-6200 Photosynthetic system) were recorded at both these stages of growth. Levels of total chlorophyll, starch, total soluble carbohydrates, soluble protein, free amino acids and nitrate reductase (NR) activity were analysed from two uppermost fully expanded leaves of plants under each treatment on aforesaid growth stages during both the years by adopting analytical methods reported earlier (Vyas *et al.* 1995). All the observations and estimations were based on four replicates of each treatment.

Plant performance was adjudged from final above-ground dry matter and grain yield. Water use efficiency (WUE) was computed in terms of grain yield per unit of water used. Harvest index (HI) was calculated by the equation: economic yield/biological yield × 100, where grain yield was taken as the numerator and total biomass (DMP + grain yield) as the denominator. Significance of the data was assessed through analyses of variance wherever necessary.

RESULTS AND DISCUSSION

Rainfall and soil moisture

The total rainfall received during 1997 was 440·0 mm and during 1998 it was 478·5 mm, much above the long time average of 360·0 mm for the region. In spite of the late onset of the monsoon in 1997 the distribution of rainfall was uniform during the crop growth period and the crop did not experience any soil moisture deficit except for terminal drought due to early withdrawal of the monsoon. The crop matured in 80 days. During 1998 the rainfall received during the cropping season (228·5 mm) was less and not uniform in distribution (Fig. 1). Consequently soil moisture decreased below availability limit at tillering (38 DAS) and again at flowering stage (45–53 DAS). Thereafter the crop also experienced terminal drought at maturation stage.

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Table 1. *Influence of N fertilization on water status of pearl millet genotypes during 1997 and 1998 at vegetative and flowering stages*

	ψ_{plant} (MPa)				Relative water content (%)			
	Vegetative		Flowering		Vegetative		Flowering	
Genotypes	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}
1997								
MH-179	−1·2	−1·3	−1·2	−1·3	84·8	83·7	81·4	80·8
HHB-67	−1·3	−1·4	−1·3	−1·6	85·2	84·1	85·7	83·3
CZ-IC-923	−1·1	−1·4	−1·3	−1·6	87·4	84·8	77·3	73·5
CZP-9604	−1·3	−1·4	−1·4	−1·5	84·0	83·8	84·7	75·4
B.P.	−1·3	−1·4	−1·5	−1·6	83·4	81·3	79·3	75·4
CZ-IC-718	−1·2	−1·3	−1·2	−1·4	84·5	84·0	82·7	76·2
Mean	−1·2	−1·4	−1·3	−1·5	84·9	83·6	81·9	77·4
S.E. (D.F. = 33)								
Genotype	0·05*		0·04*		1·01*		0·97*	
Nitrogen	0·03*		0·02*		0·59*		0·56*	
G × N	0·07*		0·05*		1·43*		1·37*	
1998								
MH-179	−2·0	−3·0	−1·2	−1·5	81·0	76·0	89·4	81·6
HHB-67	−2·5	−3·2	−1·0	−1·2	82·3	79·6	82·6	77·1
CZ-IC-923	−2·5	−3·5	−0·9	−1·3	81·6	80·3	82·8	74·0
CZP-9604	−2·2	−2·9	−1·1	−1·3	82·0	80·2	81·7	74·2
B.P.	−2·2	−3·0	−1·3	−1·7	81·0	76·9	82·3	73·3
CZ-IC-718	−2·0	−2·6	−1·3	−1·5	79·0	77·3	83·7	80·1
Mean	−2·2	−3·0	−1·1	−1·4	81·2	78·4	83·8	76·7
S.E. (D.F. = 33)								
Genotype	0·04*		0·05*		0·99*		0·60*	
Nitrogen	0·03*		0·03*		0·57*		0·34*	
G × N	0·06*		0·06*		1·40		0·84*	

B.P., Barmer population.
* Statistically significant at $P < 0·05$.

In both 1997 and 1998 the depletion of soil moisture due to evapotranspiration in the upper 100 cm profile was consistently more under the improved fertility condition as compared to the low fertility condition at all stages of growth in all the genotypes. However, for the purpose of brevity average soil moisture for the six genotypes has been presented (Fig. 1) to show the fertility effects. The data clearly indicated that crops grown under N fertilization utilized more soil moisture for their growth than those without N application during both the years. The differences in moisture extraction patterns in IF and LF plants generally widened with the progress of crop growth. The higher extraction of soil moisture under nitrogen fertilization has also been observed in maize (Bennett *et al.* 1986), Indian mustard (Vyas *et al.* 1995) as well as in pearl millet (Garg *et al.* 1993; Kathju *et al.* 1993) under limited water conditions. Furthermore, a significant increase in root growth of pearl millet due to N application under water stress has been reported earlier (Lahiri *et al.* 1973). The promotion of a deep and profuse root system by fertilization under dry conditions has been reported to help in extraction of water from deeper soil layers (Prihar & Sandhu 1987).

Water status

The plant water potential (ψ_{plant}) and relative water content (RWC) were generally lower in N fertilized as compared to unfertilized plants in all the genotypes during 1997 as well as 1998 (Table 1). However, differences due to genotypes and N application were not significant at the vegetative stage in 1997. In contrast ψ_{plant} was markedly low at the vegetative stage in 1998 due to occurrence of a dry spell at that point of time. Differences in water status of IF and LF plants became more clear at the flowering stage in most of the genotypes and ψ_{plant} and RWC decreased more in the IF plants due to higher vegetative growth and leaf area leading to greater water utilization. However, variations among genotypes, though significant, were not consistent at the two growth stages. A large reduction in ψ_{plant} and RWC in IF plants under water-limiting conditions has also been reported

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Table 2. *Influence of N fertilization on grain yield and dry matter production of pearl millet genotypes during 1997 and 1998*

	Grain yield (kg/ha)						Dry matter production (kg/ha)					
	1997			1998			1997			1998		
Genotypes	N_0	N_{80}	Mean	N_0	N_{80}	Mean	N_0	N_{80}	Mean	N_0	N_{80}	Mean
MH-179	532	1225	879	1213	1552	1382	2434	3586	3010	1815	2428	2122
HHB-67	988	1988	1488	1435	1614	1525	1665	2535	2100	1807	1856	1832
CZ-IC-923	604	1247	926	1229	1397	1313	2074	2819	2447	2569	3074	2832
CZP-9604	1019	1902	1460	1261	1369	1315	1948	3202	2575	2563	2736	2650
B.P.	1170	1951	1560	1303	1441	1372	2978	4190	3534	3193	3661	3427
CZ-IC-718	796	1384	1090	1553	1689	1621	1753	2999	2376	3108	3528	3318
Mean	852	1616	—	1332	1510	—	2125	3222	—	2509	2881	—
S.E. (D.F. = 33)												
Genotype		106·3*			66·0*			206·6*			135·4*	
Nitrogen		61·5*			38·1*			119·1*			78·1*	
G × N		150·3			93·4*			293·0			192·1	

B.P., Barmer population.
* Statistically significant at $P < 0·05$.

Table 3. *Influence of N fertilization on harvest index and water use efficiency of pearl millet genotypes during 1997 and 1998*

	Harvest index (%)				Water use efficiency (kg/ha/mm)			
	1997		1998		1997		1998	
Genotypes	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}
MH-179	17·94	25·46	38·06	38·99	1·88	3·91	4·21	5·33
HHB-67	37·24	43·95	44·26	46·51	3·21	6·64	5·04	5·56
CZ-IC-923	22·55	30·67	32·36	31·25	2·06	4·20	4·34	4·86
CZP-9604	34·34	37·26	32·98	33·35	3·40	5·79	4·50	4·72
B.P.	28·90	31·77	28·08	28·24	3·85	6·14	4·47	4·63
CZ-IC-718	31·23	31·58	32·32	32·37	2·60	4·27	5·37	5·70
Mean	28·62	33·40	34·68	35·12	2·83	5·16	4·66	5·17
S.E. (D.F. = 33)								
Genotype	1·567*		1·891*		0·065*		0·071*	
Nitrogen	0·899*		1·092		0·038*		0·041*	
G × N	2·202		2·675		0·092*		0·100*	

B.P., Barmer population.
* Statistically significant at $P < 0·05$.

in a number of crops (Radin & Parker 1979; Bennett *et al.* 1986; Kathju *et al.* 1993). However, it has been observed that tissue hydration may not be an infallible index of metabolic efficiency as IF plants despite lower plant water potential and turgescence than LF plants showed better crop performance and metabolism under rainfed conditions (Kathju *et al.* 1993).

Crop performance and water use efficiency

Genotypes Barmer population, HHB-67 and CZP-9604 provided significantly higher grain yield than others during 1997. However, DMP was highest in Barmer population, followed by MH-179 and lowest in HHB-67 (Table 2). Depending upon the genotype, N application increased the grain yield from 66·7 to 130·2% and stover yield from 36·0 to 64·3% during 1997. In contrast, during 1998 the magnitude of increase in grain yield and DMP due to N fertilization, though significant, was less and ranged from 8·4 to 27·9% for grain yield and from 6·7 to 33·7% for dry matter in different genotypes. During 1998 among the six genotypes, CZ-IC-718 and HHB-67 yielded significantly higher while DMP was significantly more in

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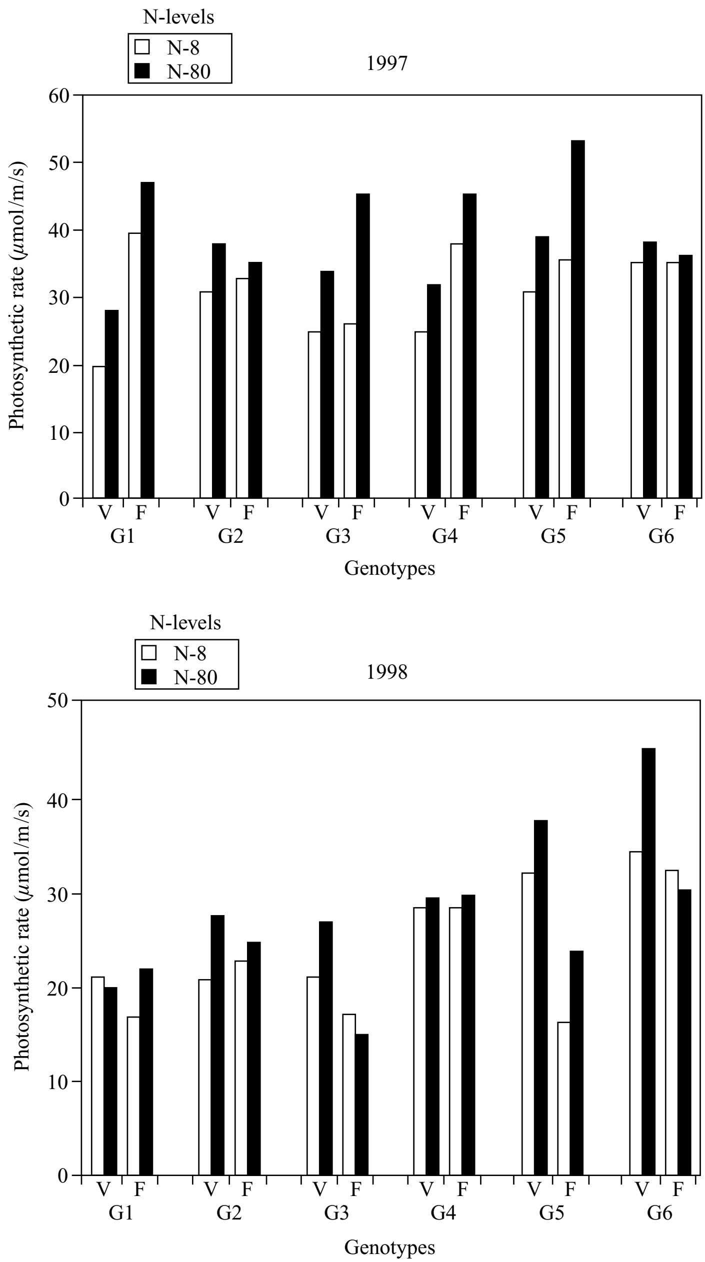

Fig. 2. Influence of N-application on net photosynthetic rate of pearl millet genotypes at vegetative (V) and flowering (F) stages during 1997 and 1998. G1–G6 indicate genotypes MH-179, HHB-67, CZ-IC-923, CZP-9604, Barmer population and CZ-IC-718, respectively. S.E.M. values for G, N and G × N in 1997 are 1·32, 0·76, 1·86 for vegetative and 1·09, 0·63, 1·54 for flowering stages. Corresponding values in 1998 were 1·24, 0·71, 1·76 for vegetative and 0·70, 0·40, 0·99 for flowering stage.

Barmer population and CZ-IC-718 than in others. The data indicated that under rainfed conditions landraces (Barmer population and CZ-IC-718) were capable of providing comparable or higher yields than hybrids and composites where improved varieties were generally not able to express their full potential. It has been generally observed that yields of modern and improved cultivars in marginal and arid environments which do not have sufficient environmental resources for the expression of a high yield potential,

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Table 4. *Influence of N fertilization on leaf area and chlorophyll content of pearl millet genotypes during 1997 and 1998 at two growth stages*

	Total chlorophyll (mg/gdw)				Leaf area (cm^2/plant)			
	Vegetative		Flowering		Vegetative		Flowering	
Genotypes	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}
1997								
MH-179	7·11	7·93	9·07	9·66	160·4	182·9	337·4	428·5
HHB-67	6·14	9·02	7·58	8·28	230·1	261·4	199·5	308·9
CZ-IC-923	6·41	6·29	7·73	8·02	136·9	207·4	304·5	480·2
CZP-9604	4·09	5·35	8·10	8·25	144·3	275·8	376·0	386·8
B.P.	5·86	8·79	8·86	9·18	181·0	299·3	228·7	348·7
CZ-IC-718	4·30	6·16	8·51	9·17	102·5	200·1	229·2	311·2
Mean	5·65	7·25	8·30	8·76	159·2	237·0	279·2	377·4
S.E. (D.F. = 33)								
Genotype	0·17*		0·40*		2·85*		5·33*	
Nitrogen	0·10*		0·23*		1·65*		3·08*	
G × N	0·24*		0·57		4·03*		7·54*	
1998								
MH-179	6·09	8·33	7·23	7·87	238·1	347·7	295·9	470·3
HHB-67	8·99	10·23	7·78	7·91	270·7	334·7	202·6	280·6
CZ-IC-923	8·48	8·70	6·61	6·93	220·4	270·4	301·4	384·0
CZP-9604	8·30	9·83	6·31	6·88	291·0	318·5	324·3	347·3
B.P.	7·50	9·65	6·51	7·01	294·2	347·1	379·8	477·4
CZ-IC-718	8·72	9·10	6·70	7·26	282·4	486·7	469·9	599·8
Mean	8·01	9·31	6·86	7·31	286·1	350·9	329·0	426·6
S.E. (D.F. = 33)								
Genotype	0·11*		0·10*		4·86*		15·62*	
Nitrogen	0·06*		0·06*		2·81*		9·02*	
G × N	0·15*		0·15*		6·88*		22·09*	

B.P., Barmer population.
* Statistically significant at $P < 0.05$.

are often disappointing (Malton 1985) and may actually be lower than those of the traditional landraces that have evolved in the area over time (Weltzien & Fischbeck 1990). Better grain and stover yields of the two landraces observed in the present study indicated adaptation to the arid zone environment as a more important determinant of yield than improved yield potential of modern cultivars. Similar observations have been made by Bidinger *et al*. (1994) working with diverse pearl millet landraces and their top cross hybrids for arid environments. It has been suggested that alleles controlling yield in such environments were different from those controlling yield in high yielding environments (Ceccarelli *et al*. 1993). Thus landraces are particularly useful for areas with unfavourable growing conditions and where stability is more important than potential yield. It was, however, noteworthy that N fertilization could significantly enhance the grain and fodder yields of landraces, though to a lesser magnitude when compared with the hybrids. N treatment also increased the harvest index in all genotypes, particularly in 1997 while such effects were less pronounced in 1998 (Table 3). Cultivar HHB-67 displayed the highest harvest index (HI) during both the years, principally due to higher grain yield associated with less biomass production indicating a better partitioning of dry matter. In general landraces had lower HI than hybrids and composites. Low HI of traditional landraces because of the biomass yield locked up in vegetative parts have been well known (Rai *et al*. 1996). However, Bidinger *et al*. (1994) reported not only high, but also comparable HI in landraces and hybrids under arid environments suggesting that grain yields were low because total plant growth was limited by lack of moisture. In the present study a greater increase in grain yield than total biomass under N fertilization probably contributed to higher HI, particularly in 1997.

Water use was comparable among genotypes and ranged from 284 to 329 mm during 1997 and from 280 to 297 mm during 1998. N fertilization marginally increased the water use in all the genotypes, more so in 1997. However, WUE was significantly and consistently increased by N application in all the genotypes mainly due to increased grain yields. The

Table 5. *Influence of N fertilization on levels of starch and total soluble carbohydrates in pearl millet genotypes during 1997 and 1998 at vegetative and flowering stages*

	Starch (mg/gdw)				Total soluble carbohydrates (mg/gdw)			
	Vegetative		Flowering		Vegetative		Flowering	
Genotypes	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}
1997								
MH-179	237·1	240·9	156·5	154·5	107·5	120·5	75·7	79·7
HHB-67	209·2	254·8	111·9	110·0	83·4	97·0	61·2	75·8
CZ-IC-923	216·4	171·2	125·0	143·2	113·8	113·6	69·8	63·9
CZP-9604	206·2	227·9	93·4	140·2	85·0	129·9	60·3	60·5
B.P.	207·8	230·5	120·7	127·1	89·9	112·6	54·2	65·5
CZ-IC-718	206·4	220·4	117·3	117·7	67·9	132·7	69·7	81·1
Mean	213·8	224·2	120·8	132·1	91·2	117·7	65·1	70·8
S.E. (D.F. = 33)								
Genotype	2·83*		3·02*		1·70*		0·85*	
Nitrogen	1·61*		1·75*		0·98*		0·49*	
G × N	3·93*		4·28*		2·40*		1·20*	
1998								
MH-179	147·3	261·4	80·6	107·4	103·6	155·3	72·6	77·7
HHB-67	165·8	195·9	80·6	120·0	106·5	135·4	60·6	71·1
CZ-IC-923	152·0	227·0	66·4	70·1	111·6	108·1	71·2	77·8
CZP-9604	231·7	305·0	74·4	83·7	112·1	124·9	74·3	61·3
B.P.	191·2	208·3	75·9	87·5	122·4	127·5	84·0	90·9
CZ-IC-718	251·2	280·7	80·5	89·9	115·2	118·0	64·8	76·2
Mean	189·8	246·0	76·4	93·1	111·9	128·2	71·2	75·8
S.E. (D.F. = 33)								
Genotype	12·87*		1·39*		2·83*		2·49*	
Nitrogen	7·43*		0·80*		1·63*		1·44*	
G × N	18·20*		1·96*		4·00*		3·52	

B.P., Barmer population.
* Statistically significant at $P < 0·05$.

magnitude of increase in WUE due to N was especially high during 1997 as compared to that found during 1998. Genotypes HHB-67 and Barmer population in 1997 and HHB-67 and CZ-IC-718 in 1998 had higher WUE than others. A number of studies have shown that greater WUE could be achieved through use of fertilizers (Onken *et al*. 1988). In his classical review on 'fertilizers and the efficient use of water', Viets (1962) concluded that in most cases when water supply was limited, a management factor that increases yield also increases WUE. Fussell *et al*. (1987) reported that improved fertility improved the WUE irrespective of its effect on water use. Similar observations have been made in pearl millet crop under arid conditions (Garg *et al*. 1993; Kathju *et al*. 1993; Siva Kumar & Salaam 1999). The beneficial effects of fertilizers could be attributed to the rapid early growth of leaves which contributes to reduction in soil evaporative losses and increased WUE (Garg *et al*. 1993; Siva Kumar & Salaam 1999). The observed leaf area enhancement by N application in the present investigation lends support to this contention.

Photosynthesis and carbohydrate metabolism

N fertilization consistently and significantly enhanced the rates of net photosynthesis in all the genotypes at both the growth stages (Fig. 2). On average the increase was 24·8 and 34·6% at the vegetative and flowering stage, respectively, in 1997. In 1998, however, it was only 16·7% at the vegetative and 11·3% at the flowering stage. Landraces Barmer population and CZ-IC-718 recorded higher photosynthetic rate during both the years at the vegetative stage. Furthermore, Barmer population and CZ-IC-718 had the highest photosynthetic rate at the flowering stage during 1997 and 1998, respectively. This was mostly associated with more leaf area in these genotypes (Table 4). Furthermore, plants grown under N fertilization had significantly greater leaf area than those without N treatment irrespective of the genotype or stage of growth. Thus N fertilization not only increased photosynthetic rate per unit area but also enhanced leaf expansion which further contributed towards overall carbon assimilation.

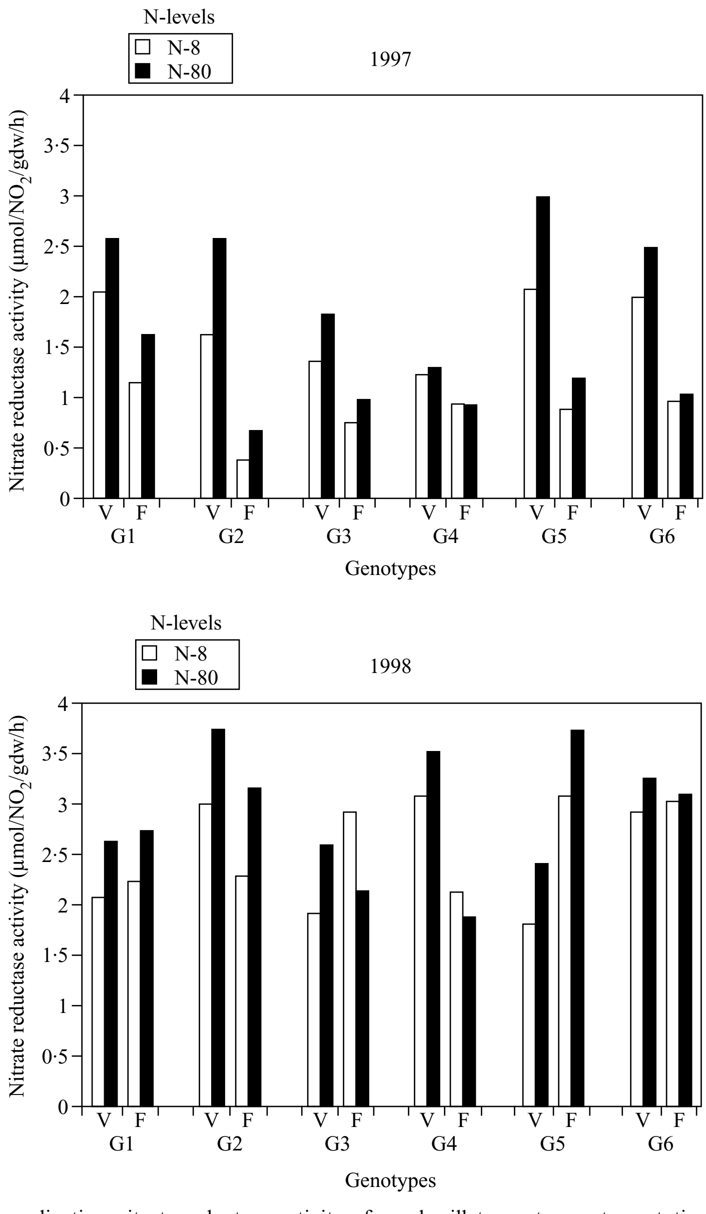

Fig. 3. Influence of N-application nitrate reductase activity of pearl millet genotypes at vegetative (V) and flowering (F) stages during 1997 and 1998. G1–G6 as in Fig. 2. S.E.M. values for G, N and G × N in 1997 are 0·043, 0·025 and 0·061 at vegetative and 0·037, 0·021 and 0·53 at flowering stage respectively. Corresponding values in 1998 were 0·044, 0·026, 0·063, 0·038, 0·022 and 0·054.

Positive yield responses due to N application were the result of increased leaf area and net photosynthesis rate per unit leaf area. Numerous studies have already demonstrated a high correlation between CO_2 assimilation per unit leaf area and leaf N content (Sinclair & Horie 1989). Likewise, close correlations have commonly been found between crop yields and N application rates (Marschner 1996). In this regard, positive interactions between water and N on leaf area development, photosynthesis and yield have also been well documented (Wolfe *et al.* 1988; Sinclair & Horie 1989). In pearl millet also, several studies indicate that N fertilization increased leaf area and chlorophyll content under rainfed conditions (Garg *et al.* 1993; Kathju *et al.* 1993; Siva Kumar & Salaam 1999). In the present study also chlorophyll content

Table 6. *Influence of N fertilization on soluble protein and free amino acids of pearl millet genotypes at two growth stages during 1997 and 1998*

	Soluble protein (mg/gdw)				Free amino acids (mg/gdw)			
	Vegetative		Flowering		Vegetative		Flowering	
Genotypes	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}	N_0	N_{80}
1997								
MH-179	42·7	50·3	20·5	18·2	10·35	14·27	9·20	10·33
HHB-67	43·6	58·4	21·3	21·5	9·96	9·62	5·92	8·29
CZ-IC-923	60·7	50·0	19·3	18·1	15·64	10·24	6·94	8·12
CZP-9604	32·2	35·9	18·3	21·6	8·45	12·96	8·09	7·26
B.P.	50·8	49·2	17·7	20·9	11·12	15·17	8·35	8·60
CZ-IC-718	49·2	53·4	22·6	21·6	11·43	16·33	7·13	8·47
Mean	46·5	49·6	20·0	20·3	11·15	13·09	7·60	8·51
S.E. (D.F. = 33)								
Genotype	2·80*		0·32*		0·28*		0·16*	
Nitrogen	1·61		0·18		0·16*		0·09*	
G × N	3·97		0·46		0·39*		0·22*	
1998								
MH-179	63·5	81·6	52·6	51·2	6·65	11·04	6·75	6·67
HHB-67	64·4	72·0	51·9	56·8	9·33	15·51	8·02	8·76
CZ-IC-923	54·2	60·5	55·3	45·0	9·44	9·51	6·30	5·79
CZP-9604	51·5	84·6	55·3	50·2	10·95	12·72	6·22	5·40
B.P.	52·0	72·8	40·9	52·3	11·22	12·27	6·65	7·82
CZ-IC-718	63·6	70·1	47·8	51·2	9·64	10·17	6·20	6·91
Mean	58·2	73·6	50·6	51·1	9·53	11·87	6·69	6·89
S.E. (D.F. = 33)								
Genotype	1·34*		1·09*		0·42*		0·47*	
Nitrogen	0·78*		0·58		0·24*		0·27	
G × N	1·90*		1·42*		0·60*		0·66*	

B.P., Barmer population.
* Statistically significant at $P < 0{\cdot}05$.

was significantly increased by N application in most of the genotypes (Table 4), irrespective of the stage of growth. Chlorophyll content was higher in genotypes HHB-67, MH-179 and Barmer population in 1997 and in genotypes HHB-67 and CZ-IC-718 during 1998 as compared to other genotypes.

N fertilization also favourably influenced the carbohydrate metabolism as the levels of both starch and total soluble carbohydrates were significantly higher in IF as compared to LF plants in all the genotypes at both the growth stages (Table 5). In general hybrids had higher levels of starch in 1997. However, genotypic differences were at variance in 1998. Both starch and total soluble carbohydrates were more at the vegetative than the flowering stage during both the years. Thus, fertilizer N-induced higher photosynthetic efficiency seems to be closely associated with a simultaneous and more efficient carbohydrate metabolism leading to higher levels of starch and total soluble carbohydrates in the fertilized plants as compared to unfertilized ones. Earlier studies with pearl millet (Kathju *et al.* 1993) and Indian mustard (Vyas *et al.* 1995) lend support to this contention.

Nitrogen metabolism

Nitrogen application significantly increased activity of nitrate reductase (Fig. 3) and levels of soluble protein and free amino acids (Table 6) in leaves of all the genotypes at both the growth stages in 1997 as well as 1998. On average, increase in NR activity was 27·6 and 25·6% at vegetative and flowering stages, respectively during 1997. However, in 1998 the corresponding increase was 20·1 and 4·8% only. Genotypes Barmer population and MH-179 during 1997, and HHB-67, CZP-9604 and CZ-IC-718 during 1998, had higher NR activity than others. Genotypic differences in N uptake and/or utilization have already been recognized in sorghum, pearl millet and wheat (Maranville *et al.* 1980; Cox *et al.* 1985; Alagarswamy & Bidinger 1987). Genetic differences in the capacity of the plant to accumulate N are very much related to the differences in NR activity (Deckard *et al.* 1973). Therefore, maintenance of high

NR activity in certain pearl millet genotypes as observed here and the marked increase in NR activity by N fertilization in all the genotypes is a pointer towards more efficient N uptake and utilization through an interaction of genotype and N. However, water limitation under arid environment may limit NR activity as this adaptive enzyme has been reported to be highly sensitive to water stress (Sinha & Nicholas 1981). The selection of a genotype with high leaf NR activity may be particularly rewarding under such conditions as more than 75% of the activity is usually found in leaves (Nair & Abrol 1979).

Soluble protein and free amino acids were higher at the vegetative stage during both the years (Table 6). The free amino acid, however, generally increased significantly due to N application except at the flowering stage in 1998. Hybrids in general showed more increase than composites and landraces due to N application in the levels of soluble protein and free amino acids. Although genotypic differences were recorded, no consistent trend was found at the two growth stages. The overall results indicate that fertilized plants maintained a more favourable nitrogen metabolism conducive for better growth and yield. These findings conform with earlier studies (Kathju *et al.* 1990, 1993; Vyas *et al.* 1995) where fertility-induced increases in NR activity coupled with higher levels of soluble protein and free amino acids were observed under limited water conditions.

The evidence presented here indicates that in dry lands where pearl millet is grown under rainfed conditions, N fertilization can augment the grain and fodder yields even when the soil moisture is limited due to recurring droughts. However, there may be greater advantages when the rainfall distribution is uniform and more favourable. The data presented did not substantiate the general belief that nitrogen fertilization under limited water conditions depleted soil moisture more rapidly through the early stages of crop growth and adversely influenced the grain yield. On the contrary fertilizer application induced better canopy development which possibly reduced wasteful evaporative water loss from the soil surface and improved water utilization by the crop, leading to a higher WUE.

Fertilizer-induced improvement of metabolic efficiency and maintenance of higher rates of photosynthesis coupled with higher nitrate reductase activity for more efficient N utilization appeared to be the control mechanism for improved performance of plants under N fertilization.

The study has also revealed significant genotypic differences in response to N and environmental conditions and the comparable yields of landraces and hybrids indicated that adaptation of these cultivars to arid conditions is a valuable characteristic for their performance under a drought situation as encountered during the period of experimentation. Maintenance of vigorous growth, high leaf area coupled with higher photosynthetic efficiency on the one hand and better N utilization and metabolism on the other might be contributing to their superior performance. However, further research on the comparative physiology of the diverse genotypes of pearl millet under water stress conditions is warranted.

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REFERENCES

Alagarswamy, G. & Bidinger, F. R. (1987). Genotypic variation in biomass production and nitrogen use efficiency in pearl millet (*Pennisetum americanum* (L.) Leeke). In *Genetic Aspects of Plant Mineral Nutrition* (Eds H. W. Gabelman & B. C. Loughman), pp. 281–286. Dordrecht: Martin Nijhoff Publishers.

Bennett, J. M., Jones, J. W., Zur, B. & Hammorst, L. C. (1986). Interactive effects of nitrogen and water stresses on water relations of field grown corn leaves. *Agronomy Journal* **78**, 273–280.

Bhatnagar, S. K., Yadav, O. P. & Gautam, R. C. (1998). Research achievements in pearl millet (*Pennisetum glaucum*). *Indian Journal of Agricultural Sciences* **68**, 423–430.

Bidinger, F. R., Weltzien, E., Mahalakshmi, R. V., Singh, S. D. & Rao, K. P. (1994). Evaluation of land races top cross hybrid of pearl millet for arid zone environments. *Euphytica* **76**, 215–226.

Ceccarelli, S., Grando, S. & Hamblui, J. (1993). Relationship between barley yields measured in low and high yielding environments. *Euphytica* **64**, 49–58.

Cox, M. C., Qualset, C. O. & Rains, D. W. (1985). Genetic variation for nitrogen assimilation and translocation in wheat. 1. Dry matter and nitrogen accumulation. *Crop Science* **25**, 430–435.

Deckard, E. C., Lambert, R. J. & Hageman, R. H. (1973). Nitrate reductase activity in corn leaves as related to yields of grain and grain protein. *Crop Science* **13**, 343–350.

De, R. & Gautam, R. C. (1987). Management practices to increase and stabilize pearl millet production in India. In *Proceeding of International Pearl Millet Workshop*, pp. 247–253. Patancheru, India: ICRISAT.

Fussell, L. K., Serajini, P. G., Bationo, A. & Kllaij M. C. (1987). Management practices to increase yield and yield stability of pearl millet in Africa. In *Proceedings of International Pearl Millet Workshop*, pp. 255–268. Patancheru, India: ICRISAT.

Garg, B. K., Kathju, S., Vyas, S. P. & Lahiri, A. N. (1993). Effect of plant density and soil fertility on pearl millet under drought and good rainfall situations. *Annals of Arid Zone* **32**, 13–20.

Garg, B. K., Vyas, S. P., Kathju, S. & Lahiri, A. N. (1984). Influence of repeated water stress on wheat. *Proceedings of the Indian Academy of Sciences* (*Plant Sciences*) **93**, 477–484.

Harinarayana, G. (1987). Pearl millet in Indian agriculture, In *Proceedings of the International Pearl Millet Workshop*, pp. 5–17. Patancheru, India: ICRISAT.

Joshi, N. L. (1984). Economics of fertilizer application in pearl millet production in arid areas. *Fertilizer Marketing News* **15**, 1–4.

Kasam, A. H. & Kowal, J. M. (1975). Water use, energy balance and growth of geromillet at Samaru, Northern Nigeria. *Agricultural Meteorology* **15**, 333–342.

Kathju, S., Garg, B. K., Vyas, S. P. & Lahiri, A. N. (1993). Effects of supplemental irrigation and soil fertilization on pearl millet under drought. *Arid Soil Research and Rehabilitation* **7**, 317–326.

Kathju, S., Vyas, S. P., Garg, B. K. & Lahiri, A. N. (1990). Fertility induced improvements in performance and metabolism of wheat under different intensities of water stress. In *Proceedings of the International Congress of Plant Physiology Vol. II* (Eds S. K. Sinha, P. V. Sane, S. C. Bhargava & P. K. Aggarwal), pp. 854–858. New Delhi: The Society for Plant Physiology and Biochemistry.

Lahiri, A. N. (1980). Interaction of water stress and mineral nutrition on growth and yield. In *Adaptations of Plants to Water and High Temperature Stress* (Eds N. C. Turner & P. J. Kramer), pp. 341–352. New York: John Wiley.

Lahiri, A. N., Singh, S. & Kackar, N. L. (1973). Studies on plant water relationships VI. Influence of nitrogen level on performance and nitrogen content of plant under drought. *Proceedings of the Indian National Science Academy* **39**(B), 77–90.

Malton, P. J. (1985). A critical review of the objectives, methods and progress to date in sorghum and millet improvement. A case study of ICRISAT/Burkino Faso. In *Appropriate Technologies for Farmers in Semi-arid West Africa* (Eds H. W. Ohm & J. G. Nagy), pp. 154–179. West Lafayette: Purdue University.

Maranville, J. W., Clark, R. B. & Ross, W. M. (1980). Nitrogen efficiency in grain sorghum. *Journal of Plant Nutrition* **2**, 577–589.

Marschner, H. (1996). *Mineral Nutrition in Higher Plants*. London: Academic Press.

Nair, T. V. R. & Abrol, Y. P. (1979). Physiological studies on nitrate assimilation and grain protein accumulation in wheat (*Triticum aestivum L.*). *Journal of Agricultural Science, Cambridge* **93**, 473–484.

Onken, A. B., Wendt, C. W. & Halvorson, A. D. (1988). Soil fertility and water use efficiency. In *Proceedings of the International Conference on Dryland farming. Challenges in Dryland Agriculture – A Global Prospective* (Eds P. W. Unger, J. V. Seed, W. R. Jordon & R. Jensen), pp. 441–444. Aurarillo/Bushland: Texas Agricultural Experimentation Station.

Prihar, S. S. & Sandhu, B. S. (1987). *Irrigation of Field Crops: Principles and Practices*. New Delhi: Indian Council of Agricultural Research.

Radin, J. W. & Parker, L. L. (1979). Water relations of cotton plants under nitrogen deficiency II. Environmental interaction on stomata. *Plant Physiology* **64**, 499–501.

Rai, K. N., Kumar, A., Andrew, D. J., Gupta, S. C. & Ouendeba, B. (1996). Breeding pearl millet for grain stability. In *Proceedings of International Conference on Genetic Improvement of Sorghum and Pearl Millet*, pp 71–83. Texas: INTSORMIL & ICRISAT.

Sinclair, T. R. & Horie, T. (1989). Leaf nitrogen, photosynthesis and crop radiation use efficiency. A review. *Crop Science* **29**, 90–98.

Sinha, S. R. & Nicholas, D. J. (1981). Nitrate reductase. In *The Physiology and Biochemistry of Drought Resistance in Plants* (Eds L. G. Paleg & D. Aspinall), pp. 145–169. New York: Academic Press.

Siva Kumar, M. V. K. & Salaam, S. A. (1999). Effect of year and fertilizer on water use efficiency of pearl millet (*Pennisetum glaucum*) in Niger. *Journal of Agricultural Science, Cambridge* **132**, 139–148.

Slatyer, R. O. & McIlroy, I. C. (1961). *Practical Microclimatology with Special Reference to the Water Factor in Soil Plant Atmosphere Relationship*. Paris: UNESCO.

Viets, F. G. Jr. (1962). Fertilizer and efficient use of water. *Advances in Agronomy* **14**, 223–264.

Vyas, S. P., Garg, B. K., Kathju, S. & Lahiri, A. N. (1995). Influence of nitrogen on Indian mustard grown under different levels of stored soil moisture. *Journal of Arid Environments* **29**, 173–184.

Weltzien, E. & Fischbeck, G. (1990). Performance and variability of local barley land races in near eastern environments. *Plant Breeding* **104**, 58–64.

Wolfe, D. S., Henderson, D. W., Hsiao, T. C. & Alvino, A. (1988). Interactive water and nitrogen effects on senescence of maize II. Photosynthetic decline and longevity of individual leaves. *Agronomy Journal* **80**, 865–870.