African Crop Science Journal,Vol. 3. No.4, pp. 433-442, 1995
Printed in Uganda.
ISSN 1021-9730/95 $ 4.00

IMPROVEMENT OF DURUM WHEAT YIELD AND ASSOCIATED EFFECTS ON MORPHO-PHYSIOLOGICAL CHARACTERS

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(Received 13 March, 1995; accepted 20 May, 1995)

ABSTRACT

Six durum wheat (*Triticum turgidum* var. *durum*) cultivars released in the central highlands of Ethiopia from 1967 to 1992, were evaluated to estimate progress in improving grain yield, and to determine changes in crop morphological and physiological attributes. The six durum wheat cultivars differed in all crop parameters studied. Over the 25 year period represented by the varietal releases, grain yield increased by 68 kg $ha^{-1}y^{-1}$ (1.58% y^{-1}). Grain yield of durum wheat was positively correlated with harvest index, grains m^{-2}, grains $spike^{-1}$, grains $spikelet^{-1}$, and thousand grain weight, all of which increased significantly over time. Spike density (i.e., spikes m^{-2}) decreased slightly while the other parameters did not exhibit significant temporal trends. Protein yield increased over time along with grain yield, while grain protein was unchanged. The national durum improvement programme has substantially improved the grain yield of rainfed durum wheat by increasing the magnitude of the grain sink and the efficiency of assimilate partitioning into grain. Durum breeders in Ethiopia should emphasise spike fertility and kernel size as reliable selection criteria for continued improvement in yield potential.

Key Words: **Breeding, selection progress, *Triticum*, yield components**

RÉSUMÉ

Six cultivars de blé dur mis au point au centre de hautes terres d'Ethiopie de 1967 à 1992, étaient évalués pour estimer l'évolution (progrès) du rendement en grains, et pour déterminer les changements morphologiques et physiologiques y afférents. Des différences significatives étaient observées parmi les six cultivars pour tous les caractères étudiées. Durant les 25 années de sélection et de diffusion, le rendement en grain a augmenté de 68kg/ha/an (1,58% par an). Le rendement en grains de blé dur était positivement correlé avec l'indice de récolte, le nombre de graines par m^2, le nombre de graines par épis, le nombre de grains par épillet ainsi que le poids de 1000 grains. Tous ces paramètres ont connu une augmentation dans le temps. La densité des épis (ex: épis par m^2) a baissé légérement durant la période de sélection, pendant que les autres paramètres n'ont pas montré une tendance significative dans le temps. La production de protéine a augmenté dans le temps ensemble avec le rendement en grains, pendant que la teneur en protéine de grains est resté inchangée.

Mots Clés: **Croisement, selection progressive, *Triticum*, composante de rendement**

INTRODUCTION

Durum wheat (*Triticum turgidum* var. *durum*), an indigenous, tetraploid species (Nastasi, 1964; Tesfaye and Jamal, 1982), is the predominant wheat species in Ethiopia, occupying up to 60% of the total national area planted to wheat (Tesfaye and Getachew, 1991). The central highlands are the major durum wheat producing region in Ethiopia (CSA, 1987), where durum wheat is traditionally grown on heavy black clay soils (Vertisols), and is produced exclusively by peasant farmers under rainfed conditions (Tesfaye and Getachew, 1991).

In Ethiopia durum wheat breeding started in 1949 at the Paradiso Experimental Station in Asmara (Nastasi, 1964). But since the early 1960s, the national durum wheat improvement programme has been situated in the central highlands at the Debre Zeit Agricultural Research Centre. Since the inception of durum breeding in Ethiopia, several durum wheat cultivars with improved yield potential, developed both from exotic germplasm and indigenous landraces, have been released and recommended for production in the central highlands of Ethiopia (Tesfaye and Jamal, 1982; Tesfaye and Getachew, 1991). The area devoted to high yielding cultivars has progressively increased as a result of these releases (Tanner and Mwangi, 1992).

This paper reports on the gains in grain yield under rainfed conditions of six durum wheat cultivars released in the central highlands of Ethiopia over the period 1967 to 1992. Furthermore, this study examines associated changes in the morphological and physiological attributes of Ethiopian durum cultivars.

MATERIALS AND METHODS

The durum yield experiment was conducted under rainfed conditions on a heavy black clay soil (pellic Vertisol) at the Debre Zeit Agricultural Research Centre (altitude 1900 m a.s.l., latitude 8° 50'N, longitude 39° 05'E) during the 1989 and 1990 cropping seasons. The climate at Debre Zeit is typical of the major durum wheat producing regions of Ethiopia (i.e., mean rainfall of 611 mm, mean minimum temperature of 10.8 °C, and mean maximum temperature of 25.8 °C during the June-November cropping cycle over the period 1975-90).

Six durum wheat cultivars, released in the central highlands of Ethiopia between 1967 and 1992, were evaluated (Table 1). DZ-04-118 is the oldest cultivar, and was developed by mass selection from a landrace population. All of the other cultivars were selections from exotic germplasm.

The experiment was laid out in a randomised complete block design with four replications. Plots consisted of 8 rows at 20 cm spacing and 5 m in length. Wheat seeds treated with aldrin were sown at the rate of 380 seeds m^{-2} in 1989 and 1990. Fertilizer was applied at a nutrient rate of 60-26 kg N-P ha^{-1} at planting, and 60 kg N ha^{-1} was top-dressed at the end of tillering of the wheat plants. The plants were allowed to grow through well-secured nylon nets to prevent lodging. Rusts and other foliar diseases were controlled by periodically spraying with triadimefon at 0.5 kg

TABLE 1. Origin, selection site, and year of release of six durum wheat cultivars included in the yield potential study

Cultivar	Origin	Selection site	Year of release
DZ-04-118	Ethiopia	Debre Zeit	1967
Gerardo[a]	CIMMYT[b]	Debre Zeit	1976
Cocorit 71	CIMMYT	Debre Zeit	1976
LD-357	USA	Debre Zeit	1979
Boohai	CIMMYT/Ethiopia[c]	Debre Zeit	1982
Foka	Ethiopia/CIMMYT[d]	Debre Zeit	1992

[a] Popularly referred to as Gerardo in Ethiopia. Full pedigree is Gerardo VZ 466/61-130 x Gll"S"
[b] International Centre for Maize and Wheat Improvement (based in Mexico)
[c] Cross made by CIMMYT; selection from F_2 made in Ethiopia
[d] Cross made in Ethiopia, using CIMMYT lines as parents

a.i. ha^{-1} and propiconazol at 0.4 kg a.i. ha^{-1}. Weeds were hand-pulled periodically.

Yield components, namely, spikes m^{-2}, grains m^{-2}, grains $spike^{-1}$, grains $spikelet^{-1}$ and spikelets $spike^{-1}$ were determined from two central rows 1 m in length, while grain and biomass yields, plant height and phenological development were measured on the central six rows of each plot. Thousand grain weights were determined for each grain sample. Grain-fill and biomass production rates, and harvest indices were calculated from the measured parameters. Grain nitrogen was determined by the micro-Kjeldahl procedure, and converted to protein using a factor of 6.25.

The average annual grain yield gain rates and the other crop parameters, were estimated by regressing the mean annual parameter values for each cultivar against the respective years of release. Correlation coefficients among the characters were computed using the annual means for each cultivar.

RESULTS AND DISCUSSION

During the growing seasons of 1989 and 1990, no unique weather conditions were observed that would have markedly affected the expression of durum wheat yield potential at Debre Zeit. Seasonal precipitation was 1.1% higher in 1989 and 8.5% lower in 1990 relative to long-term means.

There was a significant year effect on spikes m^{-2} and plant height. These characters likely responded to the slightly higher levels of precipitation, relative humidity, and sunshine hours in 1989 compared to 1990.

Cultivar by year interaction was significant only for spikes m^{-2} and spikelets $spike^{-1}$ indicating that the rankings for the other crop parameters were stable over the two seasons. For the two characters exhibiting interaction, the interaction variances were lower than the cultivar main effects. Consequently, all data were pooled for combined analyses across years. The six durum cultivars differed significantly for all of the crop parameters considered in this study.

Change in grain yield. Mean grain yield (GY) over the two cropping seasons was 4.3 t ha^{-1}. The six durum wheat cultivars exhibited a gradual increase in GY associated with the chronological sequence of release (Table 2). DZ-04-118 produced the lowest GY while the newest release, Foka, significantly outyielded all the other cultivars, representing a 56% increase in yield relative to DZ-04-118. These results agree with data from the national annual cultivar trials in which successive releases exhibited progressively higher GY (Tesfaye, 1988b).

Linear regression of the mean annual GY of cultivars on their respective years of release from 1967 to 1992 was highly significant (Table 3). The average annual increase in GY over the 25 year period from 1967 to 1992 was 68 kg ha^{-1} ($b = 0.068 \pm 0.010$ t $ha^{-1}y^{-1}$) (Fig. 1) or 1.58% y^{-1}.

The annual rate of gain in GY recorded in this study was much lower than those reported for Mexican durum wheat cultivars under irrigated

TABLE 2. Performance of six durum wheat cultivars (Debre Zeit, 1989 and 1990)

Cultivar[a]	Grain yield (t ha^{-1})	Harvest index (%)	Plant height (cm)	Grains m^{-2}	Grains $spike^{-1}$
DZ-04-118	3.19 D	23.5 C	117 C	9155 D	23.0 C
Gerardo	4.48 BC	31.5 B	94 D	11864 C	33.1 B
Cocorit 71	4.15 C	33.8 AB	87 E	13702 A	34.7 B
LD-357	4.43 BC	30.6 B	133 A	13244 AB	33.7 B
Boohai	4.57 B	32.2 A	135 A	12307 BC	34.1 B
Foka	4.99 A	36.7 A	126 B	13058 AB	37.3 A
Mean	**4.30**	**31.4**	**115**	**12222**	**32.7**
C.V. (%)	6.77	9.3	3.7	8.80	7.2

[a]cultivars are arranged from the oldest to the most recent releases.
Means within a column followed by the same letter are not signifiantly different at the 5%.

conditions (Table 4). Dramatic GY increments of 187 to 217 kg ha^{-1}y^{-1} from 1960 to 1985 (Brajcich *et al.*, 1986; Brajcich and Prescott, 1988), 251 kg ha^{-1}y^{-1} from 1960 to 1971, and 211 kg ha^{-1}y^{-1} from 1971 to 1985 (Waddington *et al.*, 1987), were reported for the durum wheat cultivars released in

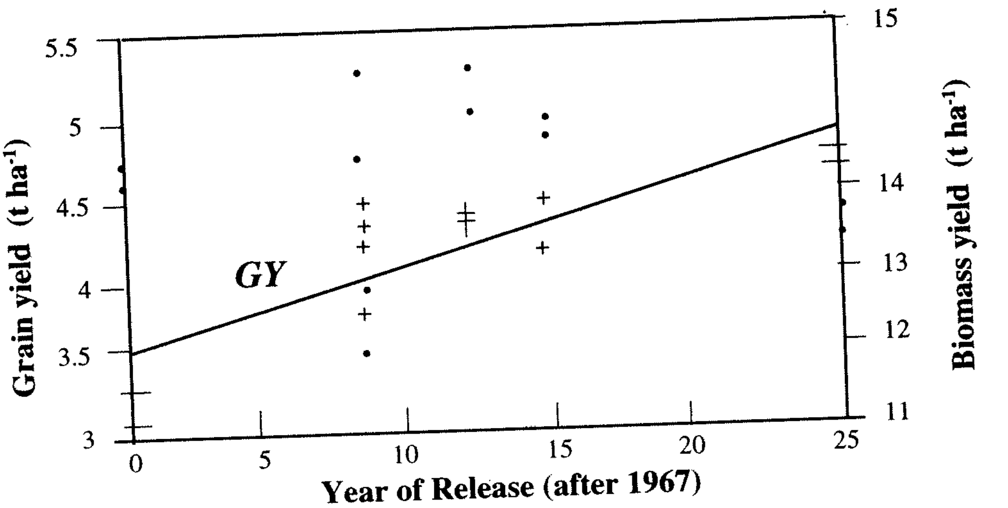

Figure 1. Grain (GY) and biomass yield of six durum wheat cultivars released in Ethiopia during 1967 to 1992 (Debre Zeit, 1989 and 1990)

TABLE 3. Linear regression for various morpho-physiological characters of durum wheat cultivar means on year of release (Debre Zeit, 1989 and 1990)

Character[a]	Mean	R^2	b
GY	4.30	79.7	0.068***
BY	13.79	2.4	0.016
HI	31.37	71.9	0.467***
PH	115.1	7.0	0.974
SM	377.2	37.9	-2.004*
TGW	33.03	63.9	0.338***
GM	12221	36.2	131.3*
GS	32.66	66.5	0.511***
SIS	18.42	14.2	-0.059
GSI	1.79	63.6	0.032***
At	69.33	2.0	-0.061
PM	109.8	0.2	0.017
GFP	40.83	1.4	0.127
SGFR	0.83	16.8	0.007
BPR	110.4	0.5	0.067
SGSFR	26.83	80.4	0.633***
TGSFR	93.29	52.6	1.197**
PGP	13.61	2.2	-0.013
PY	583.7	71.3	8.927***

[a]GY = grain yield (t ha^{-1}); BY = biomass yield (t ha^{-1}); HI = harvest index (%); PH = plant height (cm); SM = spikes m^{-2}; TGW = thousand grain weight (g); GM = grains m^{-2}; GS= grains spike^{-1}; SIS = spikelets spike^{-1}; GSI = grains spikelet^{-1}; At= anthesis (d); PM = physiological maturity (d); GFP = grain filling period (d); SGFR = single grain filling rate (mg grain^{-1} d^{-1}); BPR= biomass production rate (kg ha^{-1} d^{-1}); SGSFR = spike grain-sink filling rate (mg spike^{-1} d^{-1}); TGSFR = total grain-sink filling rate (kg ha^{-1} d^{-1}); PGP= percent grain protein (%); PY = protein yield (kg ha^{-1}).

*, **, ***: b values significantly different from zero at the 5, 1 and 0.1% levels, respectively.

TABLE 4. Rates of genetic gain in yield potential of durum wheat due to cultivar selection

Region	Period	Genetic gain[a]	Base yield[b]	Reference
Ethiopia	1967-92	67.81	3508	current study
Ethiopia	1976-92	42.50	3926	current study
Mexico	1960-71	251.00	3695	Waddington *et al.*, 1987
Mexico	1971-85	211.00	6540	Waddington *et al.*, 1987
Mexico	1960-85	217.00	3300	Brajcich and Prescott, 1988
Mexico	1960-84	187.00	3340	Brajcich *et al.*, 1986

[a] In kg ha^{-1} y^{-1}
[b] In kg ha^{-1}

Mexico. These high rates of increase for irrigated durum wheat can be attributed to the substantial investment by CIMMYT in genetically improving the initially low yielding Mexican durum germplasm (Brajcich and Prescott, 1988). In contrast, Schmidt (1984) found no significant temporal trend for durum GY over the period 1958 to 1980 due to the highly variable climatic conditions in the rainfed durum wheat growing areas of the U.S.A. Grain yield and the rate of increase in yield in the current study were lower than those reported for irrigated durum in Mexico due to the moisture-stress, under the rainfed conditions of the trials. In fact, durum wheat crops growing on Vertisols in Ethiopia commonly experience soil water-logging during early growth phases, and drought stress exacerbated by soil cracking in the latter part of the season (Tesfaye, 1988a).

Wheat GY was significantly and positively correlated with harvest index (HI), thousand grain weight (TGW), grains m^{-2} (GM), grains $spike^{-1}$ (GS), grains $spikelet^{-1}$ (GS1), spike grain-sink filling rate (SGSFR), total grain-sink filling rate (TGSFR), and protein yield (PY), and was negatively correlated only with the number of spikes m^{-2} (SM) (Table 5). Each of the above parameters exhibited significant temporal trends over the period 1967-1992 (Table 3), with rates of increase ranging from 1.07 to 2.36% y^{-1} for the positively correlated characters, and a rate of decrease of 0.53% y^{-1} for spikes m^{-2} (Table 5).

In Ethiopia, durum wheat cultivars released in the central highlands are reported to have specific geographical adaptation (Tesfaye, 1988a; Tesfaye and Getachew, 1991). Hence, to confirm the results in this study, it could be useful to conduct additional experiments at representative sites located in the major durum wheat growing areas of Ethiopia.

TABLE 5. Relative genetic gains for morpho-physiological characters and their corrrelations with grain yield for six durum wheat cultivars (Debre Zeit, 1989 and 1990)

Character[a]	Relative genetic gain (% y^{-1})	Correlation Coefficient (r)
GY	1.58***	-
BY	0.12	0.277
HI	1.49***	0.899***
PH	0.85	0.209
SM	-0.53*	-0.689*
TGW	1.02***	0.667*
GM	1.07*	0.747**
GS	1.56***	0.919***
SIS	-0.32	-0.456
GSL	1.79***	0.881***
At	-0.09	0.131
PM	0.02	0.357
GFP	0.31	0.334
SGFR	0.84	0.332
BPR	0.06	0.024
SGSFR	2.36***	0.885***
TGSFR	1.28**	0.862***
PGP	-0.10	-0.232
PY	1.53***	0.930***

[a]Refer to Table 3
*, **, ***: Significantly different from zero at the 5, 1 and 0.1% level, respectively.

Biomass yield and harvest index. Mean biomass yield and harvest index of the six durum wheat cultivars used in the yield trial were 13.8 t ha^{-1} and 31.4%, respectively.

The three most recent releases did not differ in

BY from the oldest cultivar, DZ-04-118, while Cocorit 71 had a significantly lower BY than the other five cultivars (data not shown). Thus, in contrast to GY, BY did not exhibit a significant temporal trend of varietal release considered in this study (Fig. 1).

Harvest indices differed significantly among the six durum cultivars. DZ-04-118 had the lowest HI, reflecting poor efficiency of photosynthate partitioning to the spike. Over the 25 year period of varietal improvement, HI increased by 13.2 percent. In a similar experiment conducted on durum wheat in Mexico, but under irrigated condition, Waddington *et al.* (1987) found that, for cultivars released during 1960 to 1975, HI rose by 21.8 percent. The same authors noted that the HI of cultivars released after 1975 declined due to higher biomass production.

The linear regression of HI on year of varietal release (Table 3) showed a significant temporal trend; the annual rate of gain in HI was 0.47 percent from 1967 to 1992 (Fig. 2).

Based on the mean annual values for individual cultivars, GY, was strongly and positively correlated with HI (Table 5), but did not exhibit a significant relationship with total above-ground BY. Similarly, the comparisons of old and modern wheat cultivars by Austin *et al.* (1980) and Slafer and Andrade (1989) revealed a strong positive correlations between GY and HI, but not between GY and BY.

Plant height. Durum wheat cultivars varied in height significantly (Table 2). Foka, the most recent cultivar, was 7.7% taller than DZ-04-118, the oldest cultivar included in the study. In general, however, plant height (PH) had no relation with year of varietal release (Table 3, Fig. 2). This lack of change is attributable to the fact that Ethiopian durum wheat breeders have selected against semidwarf phenotypes because of farmer preference for tall cultivars (Tesfaye and Jamal, 1982). By contrast, Ethiopian bread wheat breeders have reduced PH at a rate of 1.03 cm y^{-1} over a 38 year period of crop improvement (Amsal, 1994).

In the current study, PH was positively correlated with BY, but was not correlated with HI (Table 6).

Yield components. Grain yield exhibited a positive correlation with TGW, grains m^{-2} and its components viz grains $spike^{-1}$ and grains

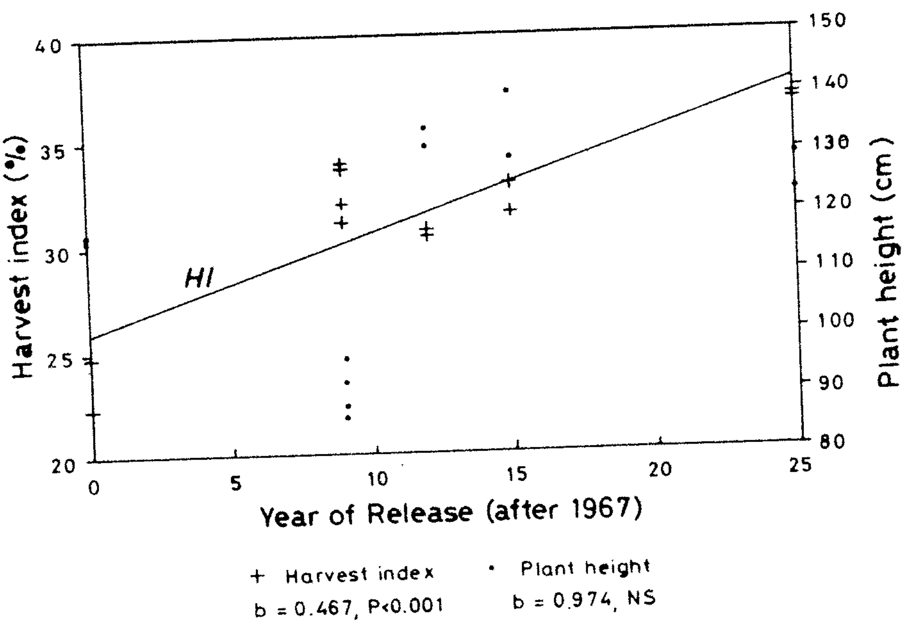

Figure 2. Harvest index (HI) and plant height of six durum wheat cultivars released in Ethiopia from 1967 to 1992 (Debre Zeit, 1989 and 1990).

TABLE 6. Correlation coefficients among selected morpho-physiological characters of six durum wheat cultivars (Debre Zeit, 1989 and 1990)

	BY[a]	HI	PH	SM	TGW	GM	GS	SIS	GSI	At	PM	GFP	SGFR	BPR	SGSFR	TGSFR	PGP
HI	-0.170																
PH	0.618*	-0.055															
SM	-0.257	-0.590*	-0.109														
TGW	0.360	0.530	0.540	-0.823***													
GM	-0.175	0.843***	-0.054	-0.153	0.151												
GS	-0.040	0.959***	0.012	-0.551	0.487	0.907***											
SIS	-0.205	-0.376	-0.434	-0.168	-0.119	-0.621*	-0.454										
GSI	0.014	0.897***	0.142	-0.381	0.429	0.939***	0.957***	-0.684*									
At	0.325	-0.028	-0.429	-0.394	-0.035	-0.193	-0.014	0.329	-0.147								
PM	-0.247	0.463	-0.722**	-0.253	-0.250	0.484	0.494	0.078	0.362	0.581*							
GFP	-0.590*	0.612*	-0.209	0.061	-0.091	0.766**	0.620*	-0.299	0.617*	-0.526	0.376						
SGFR	0.546	0.100	0.547	-0.655*	0.825***	-0.296	0.035	0.060	-0.013	0.234	-0.423	-0.606*					
BPR	0.896***	-0.376	0.798**	-0.066	0.370	-0.380	-0.283	-0.184	-0.180	0.007	-0.649*	-0.657*	0.612*				
SGSFR	0.355	0.749**	0.338	-0.846***	0.900***	0.457	0.751**	-0.276	0.690*	0.173	0.099	0.033	0.671*	0.209			
TGSFR	0.581*	0.618*	0.284	-0.764**	0.728**	0.376	0.638*	-0.299	0.592*	0.458	0.217	-0.184	0.655*	0.339	0.905***		
PGP	0.082	-0.273	-0.046	-0.125	0.094	-0.556	-0.425	0.503	-0.542	0.383	-0.216	-0.627*	0.521	0.176	-0.026	0.101	
PY	0.293	0.821***	0.181	-0.735**	0.695*	0.567	0.782**	-0.279	0.698**	0.274	0.301	0.126	0.510	0.066	0.877***	0.903***	0.140

[a]Refer to Table 3
*, **, ***: Significant at the 5, 1 and 0.1% probability levels, respectively.

spikelet^{-1} (Table 5), but negatively correlated with the number of productive spikes m^{-2}. The positive correlations with grains spike^{-1}, grains spikelet^{-1} and with TGW, could be attributed to more efficient partitioning of dry matter to the spike in the successively released cultivars. This was substantiated by the highly significant positive correlations between HI and grains m^{-2}, grains spike^{-1} and grains spikelet^{-1} (Table 6). Similar correlations were reported by Waddington *et al.* (1987), Austin *et al.* (1980), and Slafer and Andrade (1989).

The number of productive spikes m^{-2} was significantly higher for the oldest cultivar relative to their newest counterparts, indicating a 12.8% decrease (from 400 to 349 spikes m^{-2}) over the 25 years of breeding. Compared to the oldest cultivar, TGW increased by 24.2% (from 30.9 to 38.4 g) in the newest cultivar. From the linear regressions (Table 3), both characters exhibited significant temporal trends over the 25 years of varietal release. Number of spikes m^{-2} and TGW were strongly and negatively correlated (Table 6), presumably reflecting the characteristic yield compensation of wheat. TGW was not significantly correlated with BY, and showed no relation with HI or PH.

Number of grains m^{-2} for the newest cultivar increased by 42.7% relative to the oldest cultivar (Table 2). The annual rate of increase in number of grains m^{-2} was 131 grains over the period 1967 to 1992 (Table 3 and Fig. 3). The number of grains m^{-2} consists of two components, spikes m^{-2} which decreased at a rate of 0.53% y^{-1} and grains spike^{-1} which increased by 1.56% y^{-1} (Table 5). The number of grains spike^{-1} increased significantly from the oldest cultivar to the newest one (by 14.3 grains), explaining most of the variation in grain number m^{-2} (Fig. 3). This observation agrees with the report by Waddington *et al.* (1987). The annual rate of increase in the number of grains spike^{-1} was 0.511 from 1967 to 1992 (Table 3).

Grains m^{-2} showed a high positive correlation with HI (Table 6), but was not significantly correlated with BY, PH, spikes m^{-2}, or TGW. This suggested that the increase in grain number was due to improved partitioning of dry matter to the spike.

Number of spikelets spike^{-1} differed among the six durum cultivars (data not shown), but exhibited no significant change with years of varietal release (Table 3). However, the number of grains spikelet^{-1} increased at an annual rate of 0.032 from 1967 to 1992, and was closely correlated with the number of grains spike^{-1} (Table 6). This indicated that the rise in number of grains spike^{-1} resulted from an improvement in the number of grains spikelet^{-1} rather than from a change in the number of spikelets spike^{-1}.

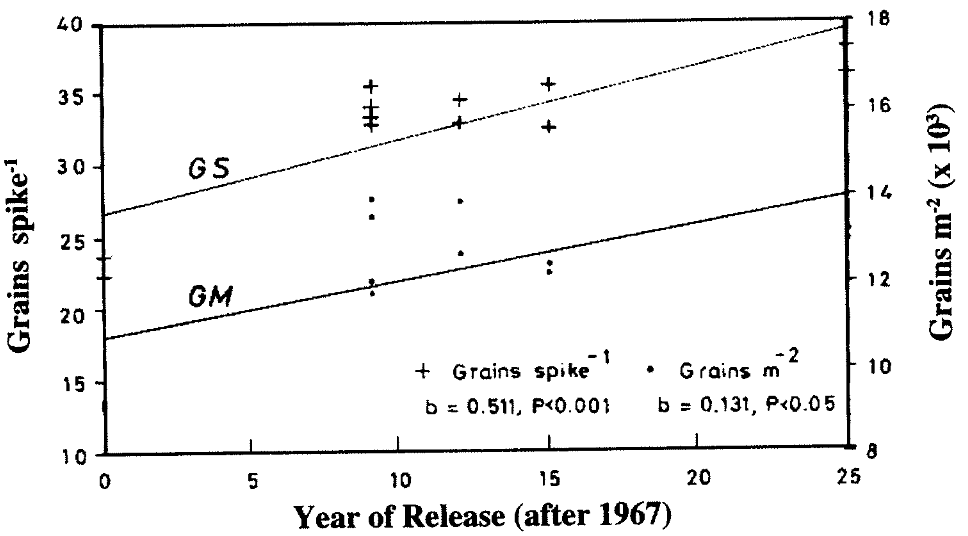

Figure 3. Grains spike^{-1} (GS) and grains m^{-2} (GM) of six durum wheat cultivars released in Ethiopia from 1967 to 1992 (Debre Zeit, 1989 and 1990).

Thus, the substantial progress in improving the grain yield of rainfed durum wheat cultivars released in the central highlands of Ethiopia over 25 years has been achieved by simultaneously improving the size of the grain sink (i.e., increased grain number m^{-2}, $spike^{-1}$ and $spikelet^{-1}$), the efficiency of assimilate partitioning into the grain (i.e., higher HI), and kernel size (i.e., TGW). Thus, durum breeders in Ethiopia should continue to utilise spike fertility and kernel size as reliable selection criteria to increase grain yield potential in the national improvement programme.

Phenology. Despite significant differences in phenological development among the six durum cultivars (data not shown), there were no significant improvement in days to anthesis (At), physiological maturity (PM), or grain filling period (GFP) over the 25 year period of varietal releases. GFP was positively correlated with HI and the number of grains m^{-2}, $spike^{-1}$, and $spikelet^{-1}$, but negatively correlated with BY (Table 6). Days to anthesis showed a significant positive correlation with PM (Table 6), while PM was negatively correlated with PH, suggesting that shorter durum cultivars took longer to reach physiological maturity.

Grain filling and biomass production rates. Single grain filling rate (SGFR) ranged from 0.85 mg $grain^{-1}$ d^{-1} for the oldest cultivar to 0.95 for the most recent release. Biomass production rate (BPR) ranged from 114 kg ha^{-1} d^{-1} for the oldest cultivar to 111 for the newest cultivar. Despite significant differences among the six cultivars, the temporal trends for these two rates were not significant (Table 3). SGFR was negatively associated with spikes m^{-2}, and positively related with TGW and BPR (Table 6). BPR was positively correlated with BY and PH, but negatively with days to physiological maturity and grain filling period.

Over the 25 year period of varietal releases, SGSFR and total grain-sink filling (TGSFR) rates increased from 19.6 to 35.4 mg $spike^{-1}$ d^{-1} and from 76.6 to 107.5 kg ha^{-1} d^{-1}, respectively, representing significant increases of 80.8 and 40.3%. Linear regression of mean rates on year of varietal release (Table 3) showed significant trends for both characters, presumably because of the improvement in grain number $spike^{-1}$ and, grains m^{-2} in the newer cultivars. The annual rate of gain from 1967 to 1992 for SGSFR was 0.63 mg $spike^{-1}$ d^{-1}, and 1.20 kg ha^{-1} d^{-1} for TGSFR. The rates of spike and total grain-sink filling were closely and positively associated with HI, TGW, grain number $spike^{-1}$ and $spikelet^{-1}$ (Table 6). This reflected the larger sink size in the recent high-yielding releases. Both parameters were significantly and negatively correlated with spikes m^{-2}.

Grain protein and protein yield. Although the six durum cultivars differed significantly in percent grain protein (PGP), this trait did not exhibit a significant temporal trend over the years of varietal release studied (Table 3). The correlation between PGP and GY was negative but not significant (Table 5). PGP was negatively correlated only with grain filling period (Table 6).

The newest cultivar had a protein yield of 688 kg ha^{-1}, 52% higher than the oldest cultivar. Linear regression of protein yield on year of varietal release (Table 3) showed a significant temporal trend for this character with an annual gain rate over the 25 years of 8.93 kg protein ha^{-1}. The correlations between protein yield and GY (Table 5), HI, TGW, number of grains $spike^{-1}$ and $spikelet^{-1}$, SGSFR and TGSFR were positive and significant (Table 6).

ACKNOWLEDGEMENTS

The research presented in this paper was conducted as part of M.Sc. programme by the first author under the sponsorship of the wheat agronomy component of the CIMMYT/CIDA East African Cereals Programme. Assistance provided by the national wheat research programme of Ethiopia under the auspices of the Debre Zeit A.R.C. of the Alemaya University of Agriculture is gratefully acknowledged.

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