Improvement of Iranian Wheat Cultivars Bred During 1956-1995 in Relation to Wild Oat Competition

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ABSTRACT

To evaluate the genetic improvement in yield of wheat (*Triticum aestivum*) bred between 1956 and 1995, a field experiment was carried out in Arak, Iran, during the 2001-2002 growing season. Six wheat cultivars, from different years of release (Omid 1956, Bezostaya 1969, Azadi 1979, Ghods 1989, Alamot 1995 and Alvand 1995) were sown with and without competition from wild oat (*Aven fatua*). The results showed a trend to increasing yield at later release dates with a rate of 2.2 % yr^{-1} and 3.8% yr^{-1} under weed free and weedy conditions, respectively. The greater yield increase obtained in weedy conditions indicates an improvement in the potential competitive abilities of new cultivars. Harvest Index (HI) and biomass were highest in new cultivars. Increased HI could explain 74% of the gain in yield, whereas, the remaining 26% of yield improvement was attributed to increases in biomass. There were no differences between cultivars in extinction coefficients (*K*) and Radiation Use Efficiency (RUE). However, RUE was reduced significantly in weedy conditions. RUE increased with the year of release by 0.77% yr^{-1} and 0.14% yr^{-1} under weed free and weedy conditions, respectively. Average RUE values of of 1.3 g MJ^{-1} (in terms of absorbed photosynthetically active radiation, APAR) and

0.83 g MJ^{-1} were estimated in weed free and weedy conditions, respectively. Leaf area index (LAI) was the only component that decreased as year of release increased.

Keywords: weed competition, radiation use efficiency, harvest index, biomass, leaf area index, extinction coefficient.

چکیده

برای ارزیابی ارقام گندم (*Triticum aestivum*.) معرفی شده در فرآینـدهای بـه‌نـژادی آن از سـال ۱۳۳۵ تـا ۱۳۷۶، یک آزمایش صحرایی در سال زراعی ۱۳۸۱-۱۳۸۰ در اراک اجرا شد. گندم ارقام امیـد، بزوسـتایا، آزادی، قدس، الموت و الوند که به ترتیب در سال‌هـای ۱۳۳۵، ۱۳۴۸، ۱۳۵۸، ۱۳۶۸، ۱۳۷۹ و ۱۳۷۹ آزاد شـده‌انـد، در رقابت و بدون رقابت با یولاف وحشی (*Avena fatua* L.) کشت گردیدند. نتایج موید رونـد صـعودی عملکـرد گندم با نرخی حدود ۲/۲٪ و ۳/۸٪ در سال به ترتیب در شرایط حضور و عدم حضور علف‌هرز بود. رونـد افزایشـی سریعتر از حالت بدون رقابت در تیمارهای با علف‌هرز بیـانگر بهبـود توانـایی رقـابتی ارقـام جدیـد بـود. شـاخص برداشت (HI) و زیست توده در ارقام جدید نسبت به ارقام قدیمی افزایش یافـت. ۷۴٪ افـزایش عملکـرد توسـط شاخص برداشت قابل توجیه بود و ۲۴٪ باقیمانده افزایش عملکرد به افزایش تولید زی‌توده نسبت داده مـی‌شـود. تفاوت معنی‌داری بین ارقام از نظر کارایی مصرف نور و ضریب استهلاک نوری (*K*) وجـود نداشـت. ولـی شـرایط حضور علف‌هرز، بطور معنی‌داری کارایی مصرف نور را کاهش داد. کارایی مصرف نور روندی فزاینده را در ارتبـاط با سال آزادسازی نشان داد و به ترتیب در شرایط حضور و عدم حضور علف هرز بـا نـرخ ۰/۷٪ و ۰/۱۴٪ در سـال افزایش پیدا کرد. کارایی مصرف نور در شرایط حضور و عدم حضور علف هرز به ترتیب برابر ۱/۳ و ۰/۸۳ گرم بـر مگاژول (بر حسب تشعشع فعال فتوسنتزی جذب شده) برآورد شد. شاخص سطح برگ تنها صـفتی بـود کـه در طی زمان روند نزولی داشت.

واژه‌های کلیدی: رقابت علف‌هرز، کارایی مصرف نور، شاخص برداشت، زیست توده، شاخص سطح برگ، ضـریب استهلاک نوری

INTRODUCTION

Analysis of crop improvement during past decades can reveal the traits that have contributed to the genetic improvement of crop cultivars. Using physiological attributes as selection criteria could even accelerate future improvement in genetic traits or help to maintain current valuable traits in new cultivars. Rate of wheat yield gains in Europe and North America due to genetic improvement have been reported to be 48 kg ha^{-1} yr^{-1} (Loss and Siddique, 1994). Increasing harvest index has been the most important improvement in winter cereals (Austin *et al.,* 1989 and Siddique *et al.,* 1989a). Up to the 1970s, higher cereal grain yield was not the result of higher biomass production. In contrast, in more recent cultivars bred for use in irrigated conditions, yield increases have been related to increased biomass production when these cultivars were planted in water limited conditions (Loss and Siddique, 1994).

Beside many other physiological and morphological characteristics, radiation use efficiency (RUE) has been studied in depth (e.g. Gallagher and Biscoe, 1978; Calderini *et al*., 1997 and Loss and Siddique, 1994) and has become an important approach for understanding crop growth and yield (Sinclair and Muchow, 1999). RUE changes in different crops have been evaluated as a function of plant density (Purcell *et al*., 2002), planting patterns (Shibles and Weber 1966), diverse environments (Manrique *et al*., 1993), water-stressed and irrigated conditions (Goyne *et al*., 1993 and O'Connell *et al*., 2004), specific leaf nitrogen (SLN), gradient in canopy (Wright and Hammer, 1994) and differences in the cultivars of the same species (Siddique *et al*., 1989b; Rosenthal and Gerik 1991; Tollenaar and Aguilera 1992; Goyne *et al*., 1993; Yunusa *et al*., 1993 and Calderini *et al*., 1997). The effects of weed competition on the RUE of crop have been studied to a lesser extent. Thus, Cavero *et al*. (1999) compared the RUE of maize and jimsonweed (*Datura stramonium* L.) growing together with that of pure crop stand and found lower, but not significantly so, RUE for the mixed stand. However, in monoculture, the RUE of maize was significantly higher than that of the weed. Barens *et al*. (1990), in a study of RUE in a mixed culture of wheat and wild oat (*Avena fatua* L.), showed that differences in canopy structure are more important than assimilatory characteristics In a study of mixed and pure stands of *Arachis pintoi* Krapov. & WC Greg.and *Digitaria* sp. intercropping had no effects on the RUE of species (Cruz and Sinoquet, 1994). In contrast, white clover (*Trifolium repens* L.) had lower RUE in mixture with ryegrass (*Lolium perenne* L.) than in a pure stand (Nassiri, 1998).

The characteristics commonly identified as making crops more competitive include rapid germination and root development, early above ground growth and vigour, rapid leaf area and canopy establishment, large leaf area development and duration, and greater plant height (Christensen, 1995; Lemerle *et al*. 2001a). Many of these characteristics act by increasing resource capture by the crop, especially by reducing light quantity beneath the crop canopy and, thereby, reducing weed seedling growth (Blackshaw, 1994). Olesen *et al*. (2004) compared competitive ability of eight wheat varieties against four grass weeds. The crop traits that affected weed suppression ability were early crop development, rapid height growth and specific leaf area. Tolerance of wheat under weed pressure was more related to factors such as the extinction coefficient and leaf area per unit N uptake.

Dry matter accumulation can be expressed as the product of photosynthetically active radiation (PAR = 400-700 nm) absorbed by the plant and the efficiency with which it is used (Goyne *et al*., 1993). The amount of Absorbed PAR (APAR) depends on leaf area index (LAI) and the light extinction coefficient (*K*), which can be described by the following equation (Rosenthal and Gerik 1991):

$$I= I_0 \times \exp (K \times LAI) \qquad (1)$$

Where I, is transmitted radiation through the canopy and I_0, is incident radiation. Dry matter and APAR are linearly related and the slope of this relationship is referred to as RUE (Rosenthal and Gerik 1991). In other words, RUE simply is the phytomass (M) produced per unit of PAR energy (A) absorbed by the crop (Gallo *et al*., 1993) as:

$$RUE = M\ (g.m^{-2})/A\ (MJ.m^{-2}) \qquad (2)$$

A wide range of RUE values from 0.73 (Gregory *et al*., 1992) to 1.81 g MJ^{-1} (O'Connell *et al*., 2004) have been reported for wheat, primarily due to the great variation in locations and experimental conditions. Yunusa *et al*. (1993) compared three wheat cultivars and found that the most recently introduced cultivars had the greatest RUE. Similarly, Siddique *et al*. (1989b) found that, RUE of wheat cultivars increased from 1.08 g MJ^{-1} for the old cultivars to 1.31 g MJ^{-1} for the most modern cultivars. Similar RUE values were measured by Gregory *et al*. (1992). In other field crops, such as maize, Tollenaar and Aguiller (1992) found higher RUE in new hybrids than in older ones. Similar results with four barley cultivars were observed by Goyne et al. (1993). In all three experiments mentioned above, canopy extinction coefficients (*K*) didn't vary among cultivars.

In contrast, Caledrini *et al*. (1997) compared seven wheat cultivars introduced from 1920 to 1990 and demonstrated no relationship between RUE and year of release. Similarly, a RUE of 1.19 g MJ^{-1} was obtained for all wheat cultivars studied by Wilson and Jamieson (1985) (quoted by Sinclair and Muchow, 1999).

Although many factors influencing crop RUE (such as those mentioned above) have been examined, the effects of weed competition on both crop yield and RUE in relation to year of cultivar release have not been elucidated. The objective of this study was to determine, under both weedy and weed-free conditions, the changes in RUE, K, LAI, HI, biomass and grain yield of six Iranian wheat cultivars released between 1956 and 1995

MATERIALS AND METHODS

A field experiment was conducted during the 2001-2002 growing season at a private farm in Arak (latitude 34°5'N, longitude 49°41'E), Iran. Six wheat cultivars, released between 1956 and 1995 were sown in weedy and weed-free conditions on

November 3rd, 2001. In weedy plots, wild oat seeds were planted at high density within and between crop rows at the time of wheat sowing. The weed seedlings were later (at two leaf stage) thinned to obtain the target density of 80 plants m^{-2}. Wheat cultivars were planted at their optimum density and nitrogen requirements (Table 1). Plots consisted of seven 6 m rows spaced 20 cm apart. The soil texture was silty loam. A factorial arrangement of weed competetion×cultivars based on randomized complete blocks design was used, and each treatment was replicated 3 times. Plots were irrigated at bi-weekly intervals. From the tillering stage up to seed setting period transmitted PAR (TPAR) and incident PAR (IPAR) (i.e. above canopy) were measured bi-weekly at solar noon using a tube solarimeter. Vertical distribution of light through the canopy was measured at 25cm intervals using the tube solarimeter placed both parallel to and perpendicular to the wheat rows. Above-ground dry matter and LAI were determined in a 0.6 m^2 area of two inner rows within each plot at the time of radiation measuring. Total dry matter (TDM) was obtained by weighing samples after oven-drying at 80 ^oC for 48 h. Based on Eq. (1), *K* was estimated as the slope of the regression ln(APAR/IPAR) on LAI, viz:

$$\ln(APAR/IPAR) = -K \times LAI \qquad (3)$$

Daily incident radiation was modelled as described by Nassiri (1998) and then multiplied by 0.5 to obtain the IPAR (Loss and Muchow, 1999). Daily radiation absorbed by the canopy was then determined from calculated *K*, IPAR and interpolated LAI measured between samplings. Using daily LAI estimates and simulated incoming PAR, accumulated APAR was calculated and regressed against TDM for each cultivar on every sampling date. Slope of the linear relationship for each cultivar indicates the RUE (Goyne *et al*., 1993). Data were subjected to analysis of variance (ANOVA) and means were separated by Fisher's least significant differences (*P=0.05*) using SAS (SAS Institute Inc., 1997). Graphs were plotted using EXCEL (Microsoft office, 2003).

RESULTS AND DISCUSSION

Extinction Coefficients (K) and LAI

The range of differences for *K* was not more than 0.2 and weed infestation had no significant effects on the cultivars' *K* value. K values for the 3 most recent cultivars (Ghods, Alamot and Alvand) were higher than those of the 3 older cultivars (Omid, Bezostaya and Azadi) whether in weed-free or weedy conditions (Table 2). Our results agreed with those of Siddique *et al*., (1989b) and Yunusa *et al*., (1993) indicating greater *K* for modern cultivars. O'Connell *et al*., (2004) reported that canopy *K* value is dependent mainly on leaf angle and Loss and Siddique, (1994) suggested that a lower *K* value indicates leaf erectness. Cavero *et al*. (1999) measured a significantly higher *K* value for *D. stramonium* (0.89) than for maize (0.49) and suggested a main characteristic allowing this weed to compete against maize is, in part, its higher *K* value.

In this study, the greater *K* values for new cultivars can be attributed the higher optimum planting density of modern cultivars (Table 1) which results in lower transmission of light to the base of the canopy. Despite the significantly lower LAI for wheat in the weedy situation it exhibited a slightly, but not significantly, higher *K* (0.68) than that (0.65) in the weed-free situation. This discrepancy can be explained by the fact that the dense population of wild oat (80 plant m^{-2}) can increase the rate of light attenuation. O'Connell *et al*., (2003) measured a *K* value of 0.82 for wheat and quoted that there was a wide range of 0.44 to 1.33 for wheat.

There was no marked variation in LAI in either weed-free or weedy conditions until nearly at the tillering stage 90 days after planting (DAP), (Fig. 1). Thereafter, up to the last sampling date (201 DAP), the LAI of the cultivars differed significantly. Under weed-free conditions Alvand (LAI 4.6) and Alamot (LAI 3.0) had the largest and lowest LAI, respectively (Table 3). While all cultivars reached their maximum LAI about 150 DAP (nearly anthesis) and declined thereafter, the peak differed considerably among cultivars. LAI lasted longer in Ghods and Alvand than other cultivars. Under weed-free conditions, old cultivars (except

Alvand) had noticeably higher LAI than recent ones and wheat LAI declined by -0.02 m^2/m^2 yr^{-1} or -0.5% yr^{-1} (R^2=0.98 $P\leq 0.01$) as illustrated with the dotted line in Fig. 3d. However, inclusion of the data for Alvand reduces the decline in LAI averaged for all cultivars very greatly (-0.002 m^2/m^2 yr^{-1} or -0.7% yr^{-1}), (Table 4). A similar trend of decreasing LAI (-0.01 m^2/m^2 yr^{-1} or -0.34% yr^{-1}) was observed in the weedy plots, where Omid, the oldest cultivar, produced the highest LAI (3.3). LAI decreased significantly under weed pressure for all cultivars except Bezostaya and Alamot, in which it remained constant. As this is simply a one year-one location study, more studies are needed to substantiate the observed trend (or trends) However, the general idea of temporal changes illustrated by the results is still valuable.

Table 1. Recommended plant density and nitrogen application for 6 wheat cultivars.

Cultivars	Year of release	Density (plant.m^{-2})	Nitrogen application (Kg.ha^{-2})*
Omid	1956	300	110
Bezostaya	1969	310	220
Azadi	1979	325	220
Ghods	1989	325	220
Alamot	1995	365	250
Alvand	1995	350	250

*N was applied at planting, early jointing and heading as urea (46% N).

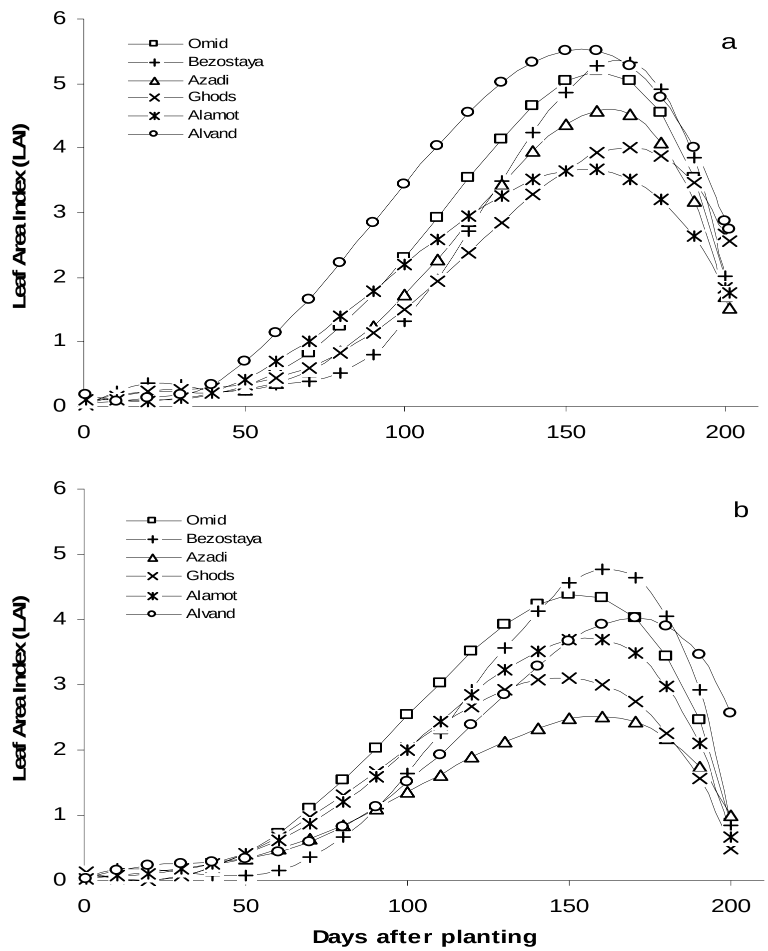

Figure 1. Leaf area index (LAI) during the growing season for each cultivar under: (a) weed-free and (b) weedy conditions.

Table 2. Radiation use efficiency (RUE g MJ^{-1}) and extinction coefficients (*K*) with their corresponding R^2 for each wheat cultivar under weed-free and weedy conditions.

Cultivars (year)	Weed free				Weedy			
	RUE	R^2	K	R^2	RUE	R^2	K	R^2
Omid (1956)	1.16	0.97	0.58	0.82	0.83	0.93	0.57	0.95
Bezostaya (1969)	1.10	0.99	0.53	0.78	0.72	0.87	0.60	0.80
Azadi (1979)	1.30	0.98	0.67	0.82	0.96	0.73	0.68	0.91
Ghods (1989)	1.80*	0.94	0.70	0.69	0.85	0.93	0.69	0.68
Alamot (1995)	1.44	0.87	0.73	0.87	0.96	0.92	0.74	0.78
Alvand (1995)	1.20*	0.95	0.71	0.68	0.71	0.93	0.77	0.70

* These cultivars varied in terms of weed conditions.

Table 3. Mean values of grain yield, biomass, HI and LAI (averaged over samplings) for each cultivar under weed-free and weedy conditions.

Cultivars (year)	Weed free				Weedy			
	Yield (Kg/ha)	Biomass (Kg/ha)	HI (%)	LAI	Yield (Kg/ha)	Biomass (Kg/ha)	HI (%)	LAI
Omid (1955)	5237	15722	34	3.87	1795	10167	17	3.31
Bezostaya (1968)	3040	12945	24	3.67	939	4178	23	3.30
Azadi (1978)	4284	15139	28	3.37	1186	8500	14	2.03
Ghods (1988)	8733	16250	54	3.20	2986	8444	36	2.37
Alamot (1994)	6637	19806	34	3.07	3104	12695	24	2.78
Alvand (1994)	7050	16195	44	4.65	2553	9017	28	2.47
LSD $_{(0.05)}$	1022	3588	6	0.76	1022	3588	6	0.76

Table 4. Yearly increase (%) in yield, HI, biomass, RUE and LAI in wheat as a result of plant breeding.

Traits	Weed- free		Weedy	
	Increase (% yr^{-1})	R^2	Increase (% yr^{-1})	R^2
Yield	2.22	0.41	3.83	0.49
HI	1.70	0.27	1.68	0.33
Biomass	0.60	0.35	0.85	0.12
RUE	0.77	0.27	0.14	0.03
LAI*	-0.07	0.01	-0.34	0.20

*Negative values for LAI indicate its decreasing trend (see text).

According to Donald and Hamblin (1976), wheat yield can be increased by increasing HI as result of decreased proportion of leaves and tillers in total biomass. Selection of wheat genotypes for Western Australia and Southwestern Iran has favored cultivars that produced fewer main stem leaves (two or three leaves) and tillers (Siddique *et al*., 1989b; Siddique *et al*., 1989b; and Yunusa *et al*. 1993) showed that old cultivars had more leaves with a prostrate orientation, a greater green area index (GAI) and a greater fraction of ground cover than modern cultivars.

Alternatively, Tollenaar (1989) presented data for maize LAI showing it increased from old to new cultivars though he did not comment on this directly. Regardless of weed conditions, LAI was not significantly correlated with most traits measured in this study (Table 5). It had a significant negative correlation with RUE (-0.47 *P=0.05*) under weed-free conditions and a positive correlation (0.56 *P=0.05*) with plant height under weedy conditions (Table 5). As will be discussed, RUE showed an increasing trend over the period of release (in contrast to LAI).

Hence the counteraction of these two processes has led in to a negative correlation between LAI and RUE.

Table 5. Correlation coefficients among five major traits measured in old and modern wheat cultivars under weed free and weedy conditions.

Traits	**Weed free**					**Weedy**				
	Yield	**Biomass**	**HI**	**RUE**	**Height**	**Yield**	**Biomass**	**HI**	**RUE**	**Height**
Biomass	0.56^{*}	1				0.74^{**}	1			
HI	0.90^{**}	0.16^{ns}	1			0.58^{*}	-0.07^{ns}	1		
RUE	0.76^{**}	0.33^{ns}	0.73^{**}	1		0.17^{ns}	0.52^{*}	-0.27^{ns}	1	
Height	-0.65^{**}	-0.15^{ns}	-0.69^{**}	-0.75^{**}	1	-0.20^{ns}	0.23^{ns}	-0.52^{*}	-0.01^{ns}	1
LAI	-0.04^{ns}	-0.18^{ns}	0.07^{ns}	-0.47^{*}	0.26^{ns}	-0.23^{ns}	-0.19^{ns}	-0.05^{ns}	-0.35^{ns}	0.56^{*}

** significant at 0.01, * significant at 0.05, ^{ns} not significant

Radiation Use Efficiency

Using daily LAI estimates and simulated incoming PAR, accumulated absorbed PAR was calculated and regressed against TDM for each cultivar for every sampling date (Fig. 2). The slope of this linear relationship indicates the RUE and is summarized in Table 2. To compare the slopes (i.e. RUE among cultivars) a pooled variance of each two regression lines (of two cultivars of interest) was calculated and then subjected to a two-tailed t-test at $P=0.05$. Ghods, with a RUE of 1.8 g MJ^{-1} , and Bezostaya, with a RUE of 1.1 g MJ^{-1}, acquired the highest and lowest RUE under weed-free conditions. Regardless of weed conditions, there were no differences among cultivars, but the RUE values of cultivars decreased significantly under weedy condition (Fig. 2b). On average, RUE in weed-free and weedy conditions was 1.3 g MJ^{-1} and 0.83 g MJ^{-1}, respectively.

Extreme reductions in the RUE of Ghods (half of its RUE in weed-free) and of Alvand under weed pressure, were responsible for the significance of this difference. However, RUE reductions in other cultivars were not significant. In weedy conditions, Azadi and Alamot had the same RUE (0.96 g MJ^{-1}which was higher than those of other cultivars. Regardless of the weed situations, the 3 most recent cultivars exhibited greater RUE than did the older ones.

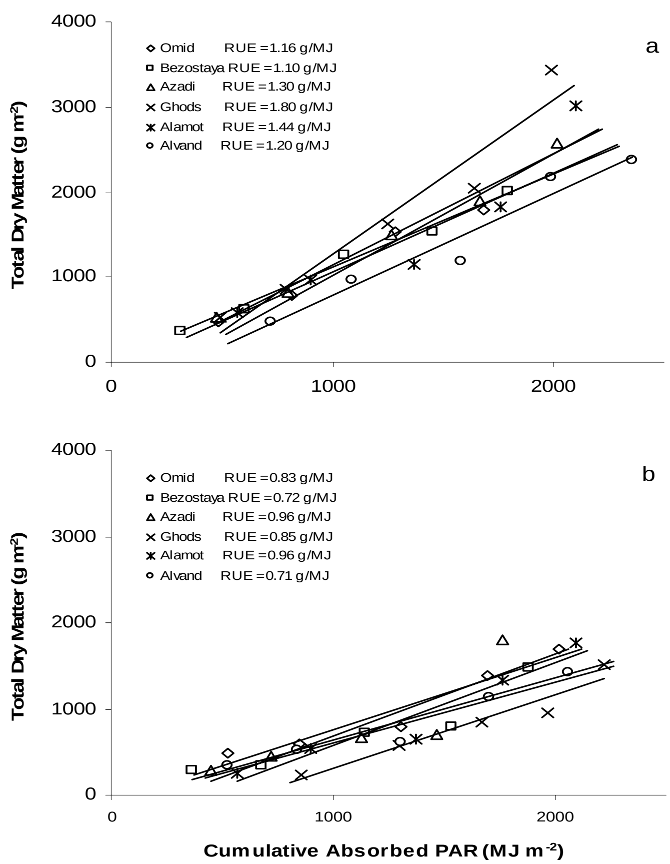

Fig. 2. Relationship between above dry matter accumulation and cumulative absorbed PAR for each wheat cultivar under: (a) weed-free and (b) weedy conditions.

(Fig 3e shows that RUE in the selected wheat cultivars has been increased in the course of breeding efforts during the period 1956 to 1995 by 0.008 g MJ^{-1} yr^{-1} or 0.77% yr^{-1} and 0.001 g MJ^{-1} yr^{-1} or 0.14% yr^{-1} in weed-free and weedy conditions respectively (Table 4). Up to 1989 (Ghods), there was an increase in RUE of 0.019 g MJ^{-1} yr^{-1} or 1.73% yr^{-1} (shown by the dotted line in Fig. 3e). Thereafter, RUE declined toward the recent cultivars Alamot and Alvand (1995)). RUE was also highly positively correlated with yield (0.76 $P=0.01$), and HI (0.73 $P=0.01$) in weed-free conditions and with biomass (0.52 $P=0.05$) in weedy condition (Table 5).

A wide range of RUE for wheat has been reported. The lowest RUE of 0.73 g MJ^{-1} was reported by Greogory *et al*. (1992), and is similar to our RUE in weedy conditions (0.83 g MJ^{-1}). O'Connell *et al*. (2003) measured a wheat RUE of 1.81 g MJ^{-1},, which corresponds to the highest value for RUE (1.80 g MJ^{-1} for cv Ghods measured by us. The estimate of 1.46 g MJ^{-1} reported by Yunnusa *et al*. (1993), based on continuous measures of radiation, may reflect potential RUE for wheat. Based on this assumption our averaged RUE of 1.3 g MJ^{-1} in weed-free conditions support their comments. Wilson and Jamieson (1985) (reviewed by Sinclair and Muchow, 1999) found no differences in RUE among wheat cultivars and obtained a common value of 1.19 g MJ^{-1}. Similarly, Caledrini *et al*. (1997) compared seven wheat cultivars and demonstrated no relationship between RUE and year of cultivar release.

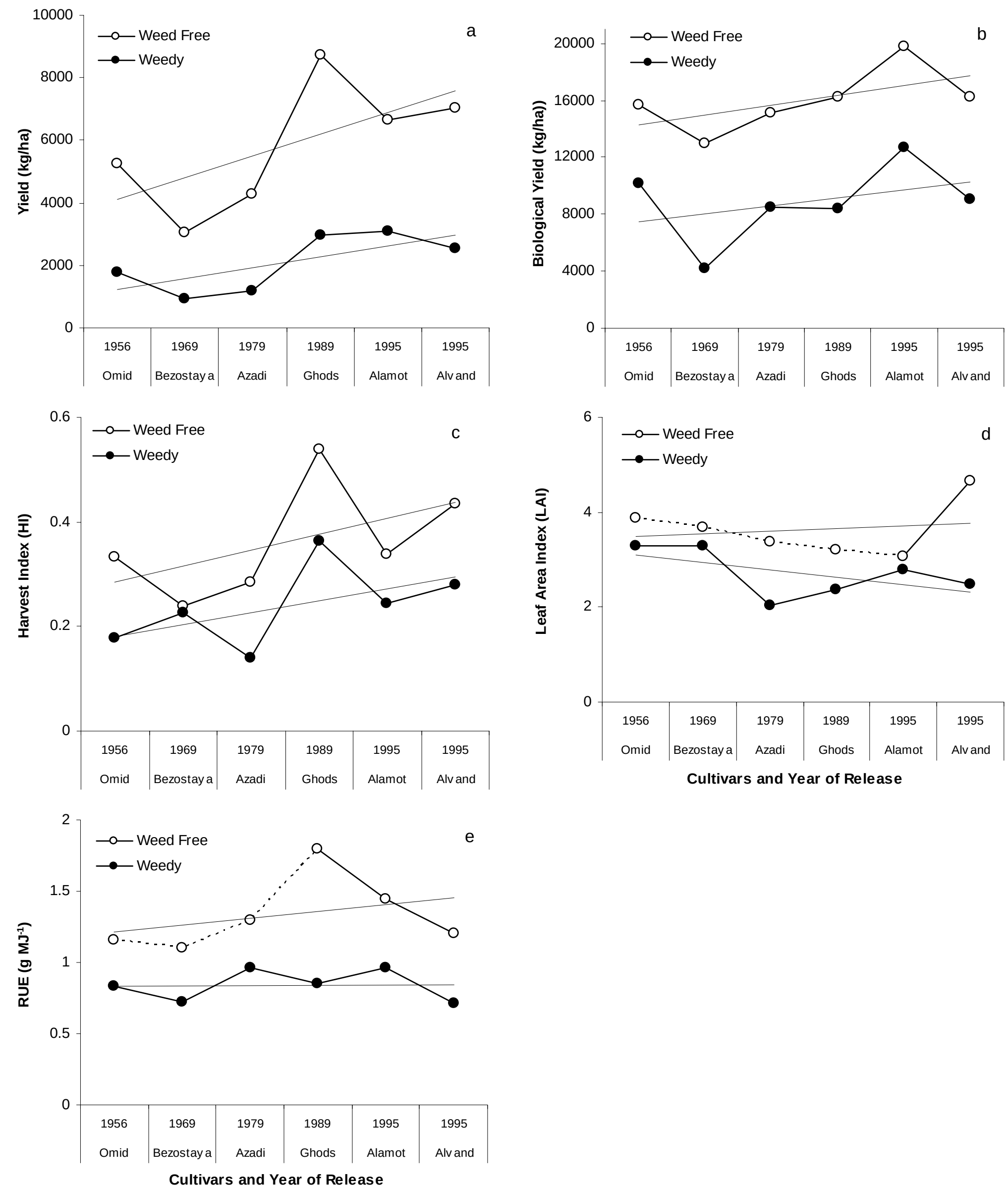

Figure 3. Changes in wheat (a) yield, (b) biomass, (c) harvest index, HI, (d) leaf area index, LAI, and (d) radiation use efficiency, RUE, under weed free and weedy conditions, in relation to the year of cultivar release. The decreasing trendin LAI up to Alamot (1995) and the increasing trend in RUE up to Ghods (1989) are depicted with dotted lines in Figs (d) and (e), respectively.

In our study, a positive relationship was observed between the year of release and RUE. Yunusa *et al*. (1993) compared three cultivars with a wide range of years of release and found higher RUE for modern cultivars. Both Siddique *et al.* (1989b) and Gregory *et al*. (1992) found that modern wheat converted intercepted radiation to above ground biomass more efficiently than older ones. It is not surprising, that RUE, as will be described later, did not vary between cultivars, as biomass accumulation was not different between cultivars at sampling dates and there was only little variation of final biomass among cultivars. As biomass is a principle source of variation in RUE, this finding means that cultivars converted light energy into dry matter with equal efficiency. Similar values of *K*, which describes the efficiency of light absorbtion by the canopy, can also explain non-significant different RUEs measured in this study. The increasing trend in RUE up to 1989 can be explained by the small increase of biomass during the same period. Competition of wild oat reduced the RUE of all cultivars, but these decreases were significant only for Ghods and Alvand. No differences in the RUE of mixed or pure stands of wild oat and wheat were observed in the study of Barens *et al*. (1990) and canopy structure/light interception relationships were more crucial than the efficiency in conversion of solar energy to dry matter by the canopy. Cruz and Sinoquet, (1994) similarly reported that intercropping of *A. pinoti* and *D. dectumbens* had no effects on the RUE of either species. Cavero *et al*. (1999) found no significant effects between maize and *D. stramonium* on the RUE of maize. Maize RUE with and without weed competition was 3.1 and 2.9 g MJ^{-1}, respectively. However, in monoculture, the RUE of maize was significantly higher than that of the weed.

Yield Changes

In both weedy and weed-free situations there were significant differences in yield of cultivars (Table 3), the 3 most recent cultivars outweighing the 3 older ones.

Ghods recorded the highest yield and Omid the lowest in weed-free conditions. A similar trend was observed in weedy conditions. Wheat grain yield decreased significantly in all cultivars when subjected to weed competition. However there were no significant difference in percent yield loss among cultivars (Fig. 4). This suggests that all cultivars possess similar competitive ability. However, this approach is misleading as when grain yield was regressed against the year of release, an upward trend toward the modern cultivars was observed for both weedy and weed-free conditions (Fig. 3a).

In this study, the average gain in grain yield was 84 kg $ha^{-1}yr^{-1}$ or 2.22% yr^{-1} and 41.5 kg $ha^{-1}yr^{-1}$ or 3.83% yr^{-1} from 1956 to 1994 under weed-free and weedy conditions, respectively (Table 4 and Fig. 3a). The higher percentage increase of yield (3.83%) in weedy conditions is due to the very low grain yield of old cultivars while new cultivars maintained a high yield. In other words, the competitive ability of cultivars has been enhanced through genetic improvements. In Western Australia, the mean yield increase due to wheat breeding was 6 kg $ha^{-1}yr^{-1}$, about one-eighth of that measured in Europe and North America (Austin *et al*., 1980 and Siddique *et al*., 1989a). The genetic gain in grain yield in maize cultivars introduced from 1959 to 1988, in Ontario, Canada, was 1.7% yr^{-1} (Tollenaar 1989).

Biomass Changes

Dry matter production at each date of sampling was not significantly different among cultivars, but final biomass varied within and among weed situations (Table 3). In weed-free conditions, only the high biomass accumulation of Alamot and Ghods were significantly different; otherwise remaining cultivars had the same biomass accumulation.

These two new cultivars also demonstrated the highest RUE (Table 2) as would be expected from their high biomass production. Similarly, cv Bezostay produced the lowest biomass and the poorest RUE (Table 2). Although, in general, the 3 most recent cultivars had higher biomass than 3 older ones, only the highest (Alamot)) and the lowest (Bezostaya) biomasses were significantly different. Approximately, the same trend was obtained in weedy conditions.

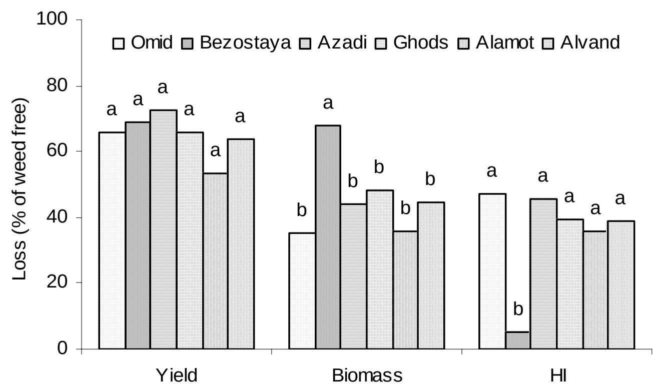

Figure 4. Percentage losses in yield, biomass and HI for each cultivar imposed by weed competition.

In the crop cultivars tested here, biomass production has increased by 84 kg ha^{-1} yr^{-1} or 0.6% and 62.5 kg ha^{-1} yr^{-1} or 0.85% under weed-free and weedy conditions, respectively (Table 4 and Fig. 3b). These values (expressed as percent) are much lower than those at which HI occurred. This characteristic has been suggested as having only a small or negligible association with yield increases achieved hitherto (e.g. Austin *et al.*, 1980; Siddique *et al.*, 1989a and Loss and Siddique, 1994).

Higher biomass can be obtained by agronomic practices such as early sowing, fertilizer application and increased plant density. Consequently, trend of the increasing biomass production observed in this study (Fig. 3b), rather than being due to the genetic manipulation for biomass accumulation per se, can be attributed to the optimum plant density and N application of new cultivars which are higher than those of old cultivars (Table 1). In the past, increases in wheat yield have largely been accomplished by a sharp rise in HI (Loss and Siddique, 1994). As Austin *et al*., 1980 estimated an upper limit of 0.62 for HI, the potential for future increases in yield through this trait is very narrow. Therefore, increasing crop biomass production should also be considered.

In this study, in weed-free conditions, HI had the highest correlation with yield (0.90 $P<0.01$), but the correlation weakened under weedy condition (0.58 $P=0.05$) where biomass showed more correlation with yield (0.74 $P=0.01$) (Table 5). In some cases, biomass of modern cultivars is greater than that of old cultivars and there has been a positive correlation between grain yield and biomass. For instance, Tollennar (1989) suggested that the observed increases in total dry matter were responsible for 85% of the genetic gain in grain yield of maize. Positive correlation of yield with biomass has also been reported for spring wheat (Hucl and Backer, 1987 quoted by Loss and Siddique, 1994).

Harvest Index Changes

HI varied significantly among treatments (Table 3). The largest value for HI was observed with Ghods, which acquired HI of 0.53 and 0.36 in weed-free and weedy conditions, respectively. For both weed-free and weedy conditions the 3 newest cultivars had higher HI than older ones. Bezostaya, with HI of 0.24 (weed-free) and Azadi with HI of 0.14 (weedy) had the lowest HI. These two old cultivars, particularly Bezostay, also produced the lowest biomass. When HI is regressed over the years of cultivar release (Fig. 3c), it is shown to have been improved from old cultivars to new cultivars by a rate of about 1.7% yr^{-1} for both weed-free and weedy conditions (Table 4). It has been suggested that the increase in HI can be due, in part, to the earlier anthesis, and reduced investment in the stem and roots, resulting from the introduction of dwarfing genes (Loss and Siddique, 1994). HI has risen from about 23% for old wheat cultivars to about 38% for modern ones (Siddique *et al*., 1989a). Our results indicate that approximately 74% of the 2.2% per year) increase of wheat yield due to genetic factors can be explained by increased HI. Consequently, 26% of this increase in yield can be attributed to the higher dry matter accumulation increases. By contrast, for maize, Tollenaar (1989) found 15% of grain yield improvement is due to HI increases.

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