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Differences in yield, biomass and their components between triticale and wheat grown under contrasting water and nitrogen environments

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ABSTRACT

A number of evidences have shown that triticale produces more above-ground dry matter (AGDM) than other winter cereals in dry environments. As AGDM accumulated by crop before anthesis has been pointed out as an important attribute under rainfed environments, the comparison of its physiological attributes (i.e. accumulated intercepted radiation – IPAR and radiation use efficiency – RUE), comparing among different cultivars and respect to other cereals, could be valuable to identify prospective traits to be used in breeding programs. Three experiments were carried out during the 2004 and 2005 growing seasons to (i) determine the effect of water stress on the yield and the eco-physiological components of biomass (i.e. accumulated intercepted radiation and RUE throughout the crop cycle) in a wide range of triticale cultivars to evaluate the genotypic variability (in interaction with water regime) for those traits and (ii) to analyze the causes for the commonly found differences in yield and AGDM between triticale and wheat under different water and nitrogen conditions. The triticale cultivars showed an important variability in yield and yield components sensitivity to drought. Water restrictions reduced AGDM, more than its partitioning to the reproductive organs, due to reductions in crop growth rate mainly through reduced RUE when different triticale cultivars were analyzed. Triticale outyielded wheat due to an increased biomass at anthesis and at maturity associated with higher RUE, probably due to a better light distribution into the canopy, more than by differences in IPAR. Triticale advantages were especially noticeable in the Mediterranean-type environment where yield and biomass were almost twice than that of wheat, associated with differences of similar magnitude in RUE.

1. Introduction

Although triticale is frequently reported to be an interesting crop for dry environments where productivity of more traditional crops such as wheat is rather limited (Ford et al., 1984), results of the literature are not uniformly consistent. For instance, under Mediterranean environments (i.e. crops growing under terminal stress, mostly during grain filling) some researchers reported that triticale seems more stress-tolerant than wheat (Sweeney et al., 1992; Giunta et al., 1993; Lopez-Castañeda and Richards, 1994; Giunta and Motzo, 2005), and in fact it has been recently proposed that introgressing "triticale traits" to wheat would increase yields (Bassu et al., 2011). On the other hand, other researchers found the opposite: wheat outyielded triticale (Fischer and Maurer, 1978; Sinha et al., 1986). Part of the inconsistency may be due to a limited genetic variation of triticales being compared to wheat in most of the above-mentioned studies.

In spite of the contrasting results in terms of yield, most literature largely agrees in that triticale produces more above-ground dry matter (AGDM) at anthesis than other cereals (Sutton and Dubbelde, 1980; Lopez-Castañeda and Richards, 1994), although exceptions are also available (Giunta and Motzo, 2005). Since dry matter accumulated by the crop before anthesis has been pointed out as an important yield-determining attribute under rainfed environments (Shepherd et al., 1987; Royo et al., 1999; Slafer et al., 2005) the identification of the physiological attributes responsible for the superiority of biomass production (i.e. accumulated intercepted radiation and radiation use efficiency) in triticale, respect to other cereals, could be valuable for breeding programs. This is particularly important taking into account that wheat yield progress in the future must be associated with increases in AGDM more than with further changes in partitioning (Shearman et al., 2005; Miralles and Slafer, 2007; Reynolds et al., 2007).

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On the other hand, harvest index has been reportedly lower in triticale than in wheat (Ford et al., 1984; Aggarwal et al., 1986; Lopez-Castañeda and Richards, 1994; Reynolds et al., 2002). Likely the inconsistent differences in yield mentioned above would be a consequence of the opposing differences in biomass and harvest index.

Yield components are differentially responsible of yield determination depending on the environmental conditions prevailing during the growing season. For example, Ford et al. (1984) and Pfeiffer et al. (1996) comparing wheat and triticale under non-limiting conditions found that the latter built the highest yield, at the expense of a higher number of grains both per unit land area and per spike. Sweeney et al. (1992) in Australia, in environments most likely suffering terminal stresses, concluded that higher yield of triticale respect to wheat was due to its heavier grains, as well as to greater number of grains per spike. On other hand, Giunta et al. (1993) and Giunta and Motzo (2005) showed that the better performance of triticale was associated with higher numbers of spikes per m^2 and grains per spike, with no clear advantages in average grain weight. The evidences reported in the literature, appear to be coincident with the fact that triticale would possess a stronger sink capacity, likely overcoming the yield limitations imposed in wheat by its frequently reported sink-limitation during postanthesis (e.g. Borrás et al., 2004 and references quoted therein). It has been demonstrated that even under Mediterranean conditions grain growth in wheat is either sink-limited (Cartelle et al., 2006) or co-limited by both source and sink strengths (Acreche and Slafer, 2009). However, the physiological bases of the hypothetically higher sink capacity and lower HI of triticale respect to wheat remain to be clarified.

The aims of this study were (i) to determine the effect of water stress on yield and the eco-physiological components of biomass (i.e. accumulated intercepted radiation and RUE throughout the crop cycle) in a wide range of triticale cultivars to evaluate the genotypic variability (in interaction with water regime) for those traits and (ii) to analyze the causes for the commonly found differences in yield and AGDM between triticale and wheat under different water and nitrogen conditions.

To fulfil the first objective 11 different commercial triticale cultivars were screened under well-watered and water stressed conditions and for the second objective single wheat cultivar was compared in two experiments with two triticales of contrasting responsiveness to stress.

2. Materials and methods

2.1. General conditions

Three experiments were carried out during the 2004 and 2005 growing seasons in the experimental field of the University of Buenos Aires (34°35′S, 59°29′W, altitude 25 m). The first experiment focused on variability among several triticale cultivars while the other two were designed to comparing a pair of triticales, which exhibited contrasting responsiveness to stress in Experiment 1, against a wheat cultivar well adapted to the region.

All experiments were conducted in the field, under the rain-shelter facility of the Institute for Agricultural Plant Physiology and Ecology (IFEVA), of the University of Buenos Aires. The soil was a 180 cm deep layer of typic argiudoll plow layer resting on native loess (Chimenti et al., 2002). An automatic watering system was used to control water supply to each of the treatments in all experiments, through a drip irrigation system with dripping lines in between the crop rows. Polycarbonate sheets of the same size than the experimental units and up to 2.5 m depth were buried along the plots for avoiding water movement among the plots.

Due to severe space restrictions within the rain-shelter facility, experimental units (sub-plots or sub-sub-plots, see below) – and thus samples taken from them – had to be small. For this reason plots in each of the three experiments were managed to be extremely uniform. The experiments were always hand-sown with a special procedure maximizing uniformity: (i) seeds (with more than 95% viability) were firstly evenly distributed in strips of sticky-tape of biodegradable paper of the same length of a row; (ii) soil was refined to minimize interference with seedling emergence, and individual furrows were opened by hand, and (iii) the strips with the seeds were placed in the furrows, covered with refined soil, (iv) the rows were lightly compacted and (v) the surface was irrigated to insure a prompt imbibition of seeds.

In the three experiments, plots were managed to minimize interferences from biotic stresses. Weeds were removed by hand, to avoid any negative effect of hormonal herbicides that may have differentially affected the cultivars. Fungicides and insecticides were sprayed throughout the crop cycle to prevent or control fungal diseases and insect damages. From the onset of stem elongation onwards nets were installed to prevent lodging.

2.2. Treatments

Experiment 1, carried out during the 2004 growing season, consisted of the factorial combination of eleven commercial cultivars of triticale and two water regimes. The cultivars included nine bred in Argentina (Remedios, Tehuelche, Presto, Yagan, Genú, Quiñe, Ñinca, Tizne and Boaglio, supplied by the National Institute of Agricultural Technology of Argentina) and two Mexican cultivars (Cerrillo and Maravilla, provided by The Autonomous University of the State of Mexico). Water regimes included a fully irrigated and drought condition, receiving 700 and 350 mm of water during the crop cycle, respectively. Water was applied throughout the crop cycle according to atmospheric demand so that the irrigated treatment received water to keep the plots close to field capacity. Amounts given at each major phase (up to the onset of stem elongation, from then to anthesis and during grain filling) are shown in Table 1. The treatments were arranged in a split-plot design with two replicates per treatment, where the water regimes corresponded to the main plots and cultivars to the sub-plots.

The experiment was hand-sown at 350 seeds m^{-2} on 21 July 2004 in sub-plots of 4 rows, 0.175 m apart and 1.4 m long (with a separation between sub-plots of 0.70 m) and conducted without nutrient limitations (150 kgN ha^{-1} were applied, and soil had 50 kgP ha^{-1}, at sowing).

Experiment 2, carried out during the 2005 growing season, consisted of a factorial combination of three genotypes (two triticales and one wheat cultivar), two water regimes and two levels of N availability. The triticale cultivars (Yagan and Tizne) were selected from Experiment 1 after showing similar durations to anthesis (1699 and 1605 °Cd, respectively; Estrada-Campuzano et al., 2008) but differential responsiveness to drought. Yagan showed higher yield reductions (60%, respect to the control), than Tizne (8%) when drought was applied (see below). The wheat cultivar (Escudo) is a commercial Argentine variety very well adapted to the region and with a cycle to anthesis (1563 °Cd) similar to that of the selected triticales. The amount of water supplied during the crop cycle was 530 and 250 mm for the irrigated and drought treatments, respectively (Table 1). Water treatments were applied using the system described above. The nitrogen availability treatments consisted of an unfertilized control (N_0) which had 115 kgN ha^{-1} at sowing in the upper 0–60 cm of soil, and a fertilized treatment (N_1) with N applied as urea at a rate of 102 kgN ha^{-1} (then equalled to an initial availability of 217 kgN ha^{-1}). The urea application was split into 2 identical quantities (51 kgN ha^{-1}) broadcasted at the beginning of tillering (DC 21, following the decimal code of Zadoks et al., 1974),

Table 1
Amount of water irrigated (mm) from seedling emergence to the onset of stem elongation (first detectable node), from then to anthesis and during post-anthesis in different treatments for each of the three experiments. The duration (days) of each of these phases, averaged across genotypes, are also given between brackets for each treatment as drought accelerated development (see Estrada-Campuzano et al., 2008).

Experiment	Treatment	Emergence to detectable node	Detectable node to anthesis	Anthesis to maturity
1	Irrigated	300 mm (65 d)	251 mm (45 d)	149 mm (34 d)
	Drought	124 mm (58 d)	150 mm (40 d)	76 mm (31 d)
2	Irrigated	253 mm (67 d)	127 mm (48 d)	150 mm (41 d)
	Drought	123 mm (62 d)	57 mm (46 d)	70 mm (36 d)
3	Mediterranean	253 mm (67 d)	127 mm (50 d)	0 mm (34 d)
	Monsoonal	123 mm (64 d)	57 mm (46 d)	150 mm (37 d)

and at the onset of stem elongation (DC 31). Application of P was not necessary due to the high P availability at sowing (46–51 ppm in the top 60 cm of the soil profile). Resource availability treatments water regimes and nitrogen levels were considered as main plots and subplots, respectively, while cultivars were assigned to sub-sub-plots under a split-split-plot design with three replicates.

The experiment was hand-sown at a density of 350 seeds m^{-2} on 27 June 2005 in sub-sub-plots of 8 rows, 0.175 m apart and 1.6 m long, with a separation between sub-sub-plots of 0.70 m.

Water content was measured gravimetrically at the stages of mid-tillering (DC 25), onset of stem elongation (DC 31), flag leaf appearance (DC 39), anthesis (DC 64), mid-grain filling (DC 75) and at physiological maturity (DC 89) to 90 cm depth. These measurements were used to calculate water accumulated in each of the stages shown in Table 1. Water content at field capacity and at permanent wilting point corresponded to 31.4 and 13.3% in volume, respectively.

Experiment 3, carried out simultaneously with Experiment 2, consisted of the same triticale and wheat cultivars (Yagan, Tizne and Escudo, respectively) grown under two regimes of water supply simulating contrasting conditions: irrigated to anthesis and then drought (Mediterranean) or drought to anthesis and then irrigated (Monsoonal). The "Mediterranean" treatment received 380 mm of irrigation up to anthesis, similar to the "irrigated" treatment of Experiment 2 for pre-anthesis, but no further irrigation was supplied thereafter; while the "Monsoonal" treatment was poorly irrigated, with only 180 mm, up to anthesis and afterwards another 150 mm were supplied during grain filling, similar to water added during grain filling in the irrigated treatment of Experiment 2 (Table 1). For the experimental design, the water regimes treatments were considered as sites and within each of them plots with cultivars were distributed in a randomised complete block design with three replicates. The experiment was hand-sown at a density of 350 seeds m^{-2} in plots of 8 rows, 0.175 m apart and 1.6 m long (plots were separated by 0.70 m). The experiment was carried out without nutrient limitations while weeds, diseases and pests were controlled as described above.

2.3. Measurements

In all experiments developmental stages were registered from seedling emergence to anthesis when 50% of the plants in the plot had reached the particular stage. To determine the stage of terminal spikelet initiation in the apex, three randomly selected plants per experimental unit were sampled once or twice a week and the main shoot apex dissected to determine its stage of development under binocular microscope following the scale of Kirby and Appleyard (1984).

Once the terminal spikelet stage was reached, three spikes per experimental unit were randomly selected and sampled twice a week until anthesis in Experiment 2 to determine the developmental progress of different floret primordia towards becoming fertile florets at, or degenerating and dying before, anthesis (as in González et al., 2003). For this purpose, in each sample the spike was divided into basal, central and apical spikelets and in each of these spikelets the floral developmental stage attained by all floret primordia differentiated was determined under a binocular microscope following the scale developed by Waddington et al. (1983), which recognizes stages from a very rudimentary floret (stage 3: glume primordium present) to a competent, fertile floret (stage 10: style curve outwards and stigmatic branches spread wide, pollen grains on well-developed stigmatic hairs).

Physiological maturity (PM) was determined as the timing when grain growth ceased, spikes from twenty main-shoots within each plot were randomly tagged at anthesis with the objective of determining the dynamics of grain filling. Dry weight (60 °C for 72 h) of the two grains most proximal to the rachis of the four central spikelets of one spike was recorded twice weekly from 7 days after anthesis onwards. The rate and duration of grain growth were estimated by fitting these dry weights against thermal time after anthesis with a bi-linear model (Eq. (1); as in Miralles and Slafer, 1995) using curve-fitting software (Jandel, 1991) that works throughout an optimization technique to determine the lines of best fit and the break-point between them. The model used was:

$$Y = a + bx(x \leq c) + bc(x > c) \tag{1}$$

where Y is grain weight, a is the intercept, b is the rate of grain filling, x is the thermal time (base temperature 0 °C) after anthesis and c is the duration from anthesis to physiological maturity. The effective duration of grain filling was obtained as [$c-(-a/b)$].

AGDM was determined from plants harvested (at different times of the crop cycle depending of the experiment) in 0.105 m^2 of the two central rows of the plots, leaving 0.15 lineal meters respect to ends of the experimental units and subsequent samples within them, and weighed after oven-dried at 60 °C for 72 h.

In Experiment 1 the values of AGDM accumulated during pre- (AGDM$_{pre-anthesis}$) and post- (AGDM$_{post-anthesis}$) anthesis and their integration (AGDM$_{cycle}$) were calculated from samples taken at anthesis and maturity. In Experiments 2 and 3 the AGDM was measured at mid-tillering, onset of stem elongation, flag leaf appearance, anthesis, mid grain filling and physiological maturity, together with soil water content determinations. In each sampling the plant material was separated into the stems, leaves (green and senescent), and spikes (when present). To determine leaf area index (LAI), only green leaves (or part of them) were passed through the electronic leaf area meter (LI 3100, Licor Inc., Lincoln, NE, USA) and this area was expressed as a fraction of the corresponding land area.

In Experiments 2 and 3, where frequent measurements of LAI were made, the coefficient of light attenuation (k) was estimated for each treatment (cultivar × water × nitrogen) based on the exponential relationship between the proportion of the incident radiation intercepted by the canopy (IPAR%) and LAI (Eq. (2)):

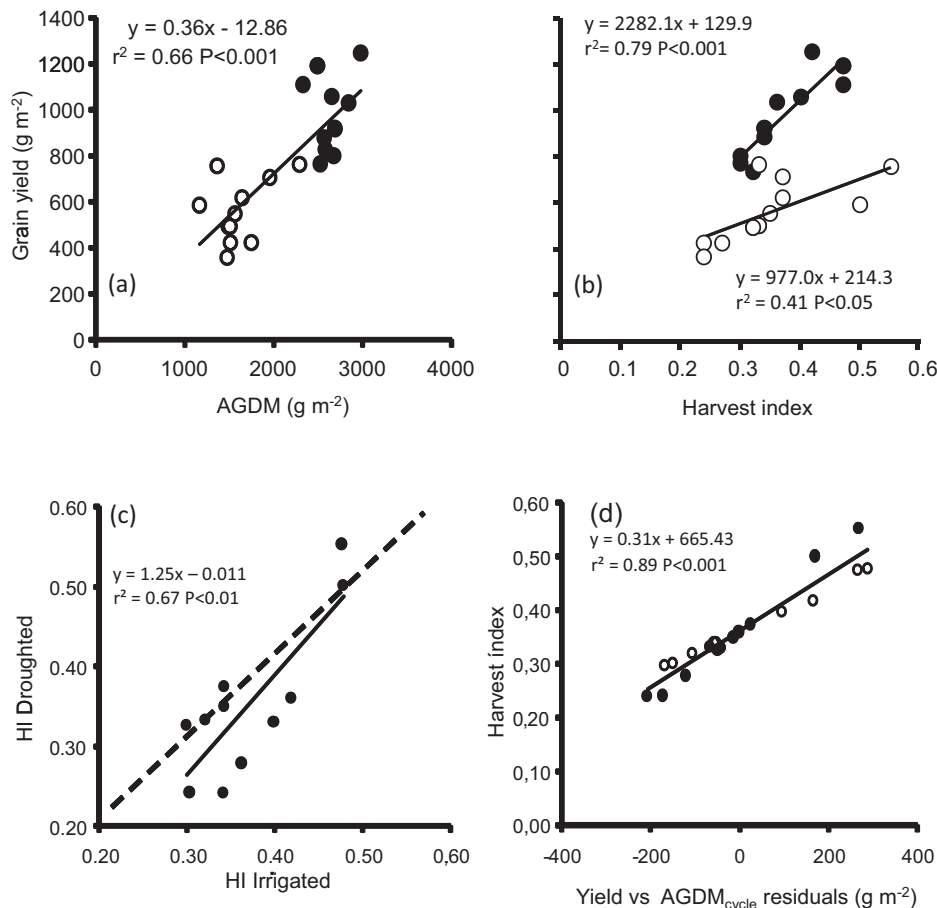$$IPAR\% = 1 - \exp^{(-k \cdot LAI)} \tag{2}$$

Fig. 1. Relationships between grain yield and above-ground dry matter ($AGDM_{cycle}$) (a) and harvest index (HI) (b), harvest index under droughted vs. irrigated conditions (c) and HI plotted against the residuals obtained from the regression between yield and above-ground dry matter ($AGDM_{cycle}$) (d) for 11 triticale cultivars grown under well irrigated (closed symbols) and under drought (open symbols). Data correspond to Experiment 1.

2.4. Estimation of intercepted photosynthetically active radiation

Photosynthetically active radiation interception (IPAR) was measured two times a week during whole cycle with a 1 m long PAR quantum sensor (LI-191 S, Li-Cor Inc., Lincoln, NE, USA) between 12:00 and 14:00 h on clear days. For this purpose, for each individual plot the line quantum sensor was placed just above the canopy level to determine incident PAR (I_0) and at the same time at the level of the senescent leaves to record the transmitted PAR (I_t), as the average of three measurements taken just above the level of the senescent leaves (on the soil when there were no senesced leaves), placing the sensor on the left, in the centre and on the right positions of the inter-row space. To determine the radiation intercepted during the crop cycle, sigmoid models were fit to the points of daily intercepted radiation to obtain the dynamics of intercepted radiation and then to calculate the cumulative radiation for each phase. The fraction of PAR intercepted at midday (F) was calculated as $(I_0 - I_t)/I_0$. Daily fraction interception (F_D) was calculated as indicated in Eq. (3) (Charles-Edwards and Lawn, 1984):

$$F_D = \frac{2F}{1+F} \tag{3}$$

and applied to corresponding daily integrals of PAR to estimate intercepted PAR (IPAR). Daily incident PAR was calculated as the incident total solar radiation measured with a standard weather station 50 m from the plots multiplied by 0.48 (Demotes-Mainard and Jeuffroy, 2004). Daily values of intercepted PAR were summed

from seedling emergence to anthesis ($IPAR_{pre-anthesis}$), from then to maturity ($IPAR_{post-anthesis}$) or both together ($IPAR_{cycle}$).

In Experiment 1 radiation use efficiency (RUE) was determined for the whole cycle and for pre- and post-anthesis periods as the quotient between the corresponding values of AGDM and the IPAR (e.g. $RUE_{pre-anthesis} = AGDM_{pre-anthesis}\ IPAR_{pre-anthesis}^{-1}$, and so on). In Experiments 2 and 3 RUE (pre- and post-anthesis or cycle) was determined as the slope of the relationship between the cumulative AGDM and the corresponding accumulated IPAR. For the calculation of the $RUE_{pre-anthesis}$ and RUE_{cycle} the relationship between AGDM and IPAR was forced through the origin.

Crop growth rates (CGR) were estimated as a ratio between the difference in AGDM and time (Experiment 1) or as the slope of a regression between the cumulative AGDM and time (Experiments 2 and 3) as in Experiments 2 and 3 samples of aerial biomass were taken throughout the experiments. At physiological maturity plants were separated in main stems and tillers and biomass, yield, yield components (number of spikes per unit land area, grains per spike, grains per m^2, averaged grain weight), and harvest index were determined.

At anthesis, beyond the samples for dry matter, five main-shoot spikes were randomly sampled and the total number of fertile florets and the number of spikelets were counted and the spike dry weight determined.

Daily air temperature and incident photosynthetic active radiation (PAR) data were recorded hourly using an automatic meteorological station (Davis, weather monitor II, USA) installed within the experimental area. With temperature data thermal time
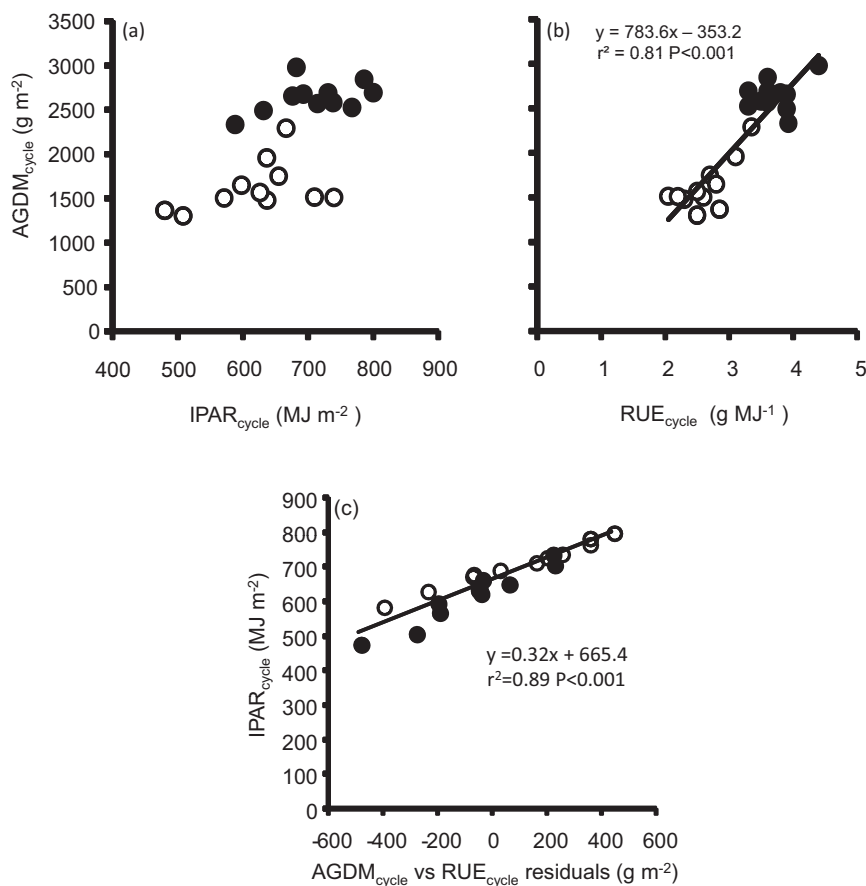
Fig. 2. Relationships between above-ground dry matter ($AGDM_{cycle}$) and intercepted photosyntetically active radiation (IPAR) (a) and radiation use efficiency (RUE) (b) and relationship between cumulative intercepted radiation during the crop cycle ($IPAR_{cycle}$) and the residuals of the regression between $AGDM_{cycle}$ and radiation use efficiency (RUE_{cycle}) for 11 triticale cultivars grown under well irrigated (closed symbols) and under drought (open symbols). Data correspond to Experiment 1.

from seedling emergence was estimated for each treatment using 0 °C as base temperature.

2.5. Statistical analysis

Analyses of variance for the design with main factors allocated to sites were performed for all variables using the appropriate model according to the experimental design used in each experiment, as described above. When the analysis of variance revealed significant differences, the mean treatment values were compared using honest significant difference (HSD) of the Tukey test using for each comparison the appropriate error term from analysis of variance (Little and Hills, 1983). The coefficients of light attenuation (k) of different treatments were compared using 95% confidence intervals. The relationships between variables were done using the linear regressions (Jandel, 1991).

3. Results

3.1. Genotypic variability among triticale cultivars

There were large variations among triticale cultivars in yield under both water regimes. Yield ranged from 3.6 to 7.6 Mg ha^{-1} under drought conditions and from 7.6 to 12.5 Mg ha^{-1} when the crop was grown under irrigation (Fig. 1a). As HI was not affected by drought, the significant reduction observed in yield (57% averaging across cultivars) was mainly associated with significant reductions in biomass (Fig. 1a). This is why when considering both environments, variations in yield were largely better explained by changes

in biomass ($r^2 = 0.66$, $P < 0.001$) than in HI, which only explained a small proportion of the variation in yield ($r^2 = 0.26$, $P < 0.01$). When HI under irrigated conditions was regressed against the HI obtained under drought, the slope was slightly higher than one as five cultivars were below the 1:1 ratio (Fig. 1c). On the other hand, although the HI was correlated to the deviations of the regression line between grain yield and total biomass the HI values were uniformly distributed along the range (positive and negative) of the residuals demonstrating that variations in HI were associated more with genotypic variations within each water regimes than with variation between water regimes (Fig. 1d). Although the relationship between yield and HI was sharper when cultivars were compared under irrigated conditions, it was still significant under drought (Fig. 1b). Additionally, within each water regimes there was not relationship between yield and biomass ($r^2_{\text{irrigated}} = 0.04$, $P > 0.10$ and $r^2_{\text{drought}} = 0.19$, $P > 0.10$). In line with what was observed in biomass, CGR_{cycle} was significantly diminished by water stress (ca. 36%, $P < 0.01$). Thus, while CGR_{cycle} ranged from 18.5 to 22.4 g day^{-1} m^{-2} in irrigation, when plants were grown under drought it ranged from 11.7 to 15.3 g day^{-1} m^{-2} (Fig. 1).

With the exception of the Mexican cultivars Cerrillo and Maravilla, which showed an extremely short cycle up to physiological maturity (see Estrada-Campuzano et al., 2008), the range of $IPAR_{cycle}$ was similar among genotypes in both water regimes (i.e. between 600 and 800 MJ m^{-2}; Fig. 2a). Then most important effects of drought operated via reductions in radiation use efficiency (RUE_{cycle}), averaging 3.7 g MJ^{-1} ($r^2 = 0.89$, $P < 0.001$) in well watered conditions and 2.6 g MJ^{-1} ($r^2 = 0.88$, $P < 0.001$) under drought; and this effect overrided that of $IPAR_{cycle}$ when both
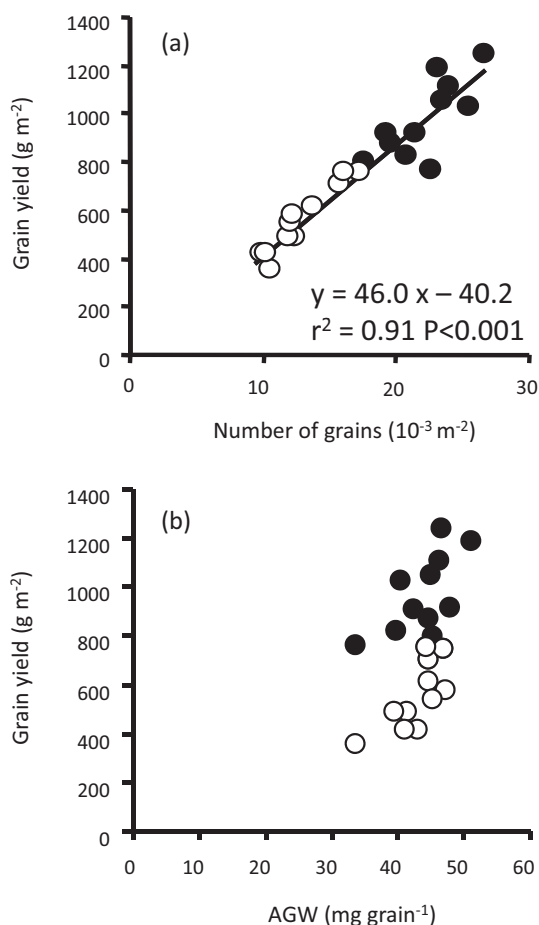
Fig. 3. Relationships between grain yield and both grain number per unit land area (a) and average grain weight (AGW, b) for 11 triticale cultivars grown under well irrigated (closed symbols) and under drought (open symbols). Data correspond to Experiment 1.

environments were considered together (Fig. 2b). There was a close association between $IPAR_{cycle}$ and the residuals of the regression of $AGDM_{cycle}$ vs. RUE_{cycle} indicating that although overall differences in $AGDM_{cycle}$ were mainly due to differences in RUE_{cycle} for genotypic differences within each water regimes (and particularly so under irrigation) were explained by changes in $IPAR_{cycle}$ (Fig. 2c).

The effects of treatments on $IPAR_{cycle}$ and RUE_{cycle} were due to aggregated effects on pre- and post-anthesis phases (Table 2), being drought effects on RUE in each period more important than those in IPAR. The determination coefficients when AGDM was regressed against RUE were significant ($r^2 = 0.59$, $P < 0.001$ and $r^2 = 0.86$, $P < 0.001$, for the pre- and post-anthesis periods, respectively). Under irrigated condition, the $RUE_{pre-anthesis}$ and $RUE_{post-anthesis}$ were very similar (ca. $3.7\,g\,MJ^{-1}$, averaging across cultivars). A similar pattern between the $RUE_{pre-anthesis}$ and $RUE_{post-anthesis}$ was observed under drought condition (2.6 and $2.5\,g\,MJ^{-1}$, respectively). However, important differences were found between RUE pre- and post-anthesis in some cultivars. For example, under the irrigated condition cultivars Remedios and Boaglio showed a large increase in $RUE_{post-anthesis}$ respect to $RUE_{pre-anthesis}$, while the reverse was observed in Genú, Quiñe and Ñinca.

Both genotypic differences and irrigation effects on yield were related to the number of grains per unit land area (Fig. 3a). The averaged weight of grains (AGW) was co-responsible for the irrigation effects on yield; but within each water regime it explained yield differences between cultivars far less than grains per m^2 (Fig. 3b). Genotypic variations in AGW were better explained by differences

in the rate of grain filling ($r^2 = 0.53$ $P < 0.001$), than in grain filling duration ($P > 0.1$).

Regarding the determinants of the number of grains per m^2, both the number of grains per spike and the number of spikes per m^2 explained the combined effects of treatments on the number of grains per m^2 (Fig. 4a and b). This was also the case for the differences among cultivars within each water regime (Fig. 4a and b). In both cases (Fig. 4a and b), the intercepts were negative implying that in general (due to cultivars differences or to irrigation) whenever the number of grains per m^2 was increased, both of its numerical components were jointly contributing to this increase. Considering both the coefficients of determination of their relationships with grains per m^2, and their ranges of variation, it seemed that overall the influence of grains per spike was slightly more determinant than that in spikes per m^2 (Fig. 4a and b).

Genotypic differences in grains per spike were associated with those in number of fertile spikelets per spike, as the number of fertile florets per spikelet was similar for all genotypes. These differences seemed to have been born in both the number of florets that were fertile at anthesis and the proportion of them that set grains, with a general trend to increase the likelihood of a fertile floret to set a grain in parallel with genotypic differences in number of fertile florets (Fig. 4c). The trends were similar under both water regimes and therefore the number of fertile florets at anthesis, and grains at maturity, per spike were higher under irrigation than under drought (Fig. 4c). Variations in the number of fertile florets per spike were in turn explained by differences in both dry weight of the spikes at anthesis (trend in Fig. 4d) and fruiting efficiency (i.e. that with which each unit of spike weight at anthesis is converted into fertile florets, graphically the residuals of the regression in Fig. 4d), particularly under irrigated conditions.

3.2. Comparison between triticale and wheat under contrasting N and water environments

As it was indicated in Section 2, the triticale cultivars Yagan and Tizne were selected to be compared with wheat, when both species were grown under different environments, due to their similar phenology but different response to water regimes. While under irrigation Tizne and Yagan showed yields of 828 and $1029\,g\,m^{-2}$, respectively; under drought yields were 762 and $422\,g\,m^{-2}$, respectively. Thus, while both cultivars recorded the same flowering time, yield reductions due to drought were 8 and 60% for Tizne and Yagan, respectively. When both triticale and wheat were analyzed under different water condition, results showed that intercepted radiation was not significantly affected by drought under non-limiting nitrogen condition but the reverse was observed under nitrogen shortage (Table 3). Triticale produced more biomass than wheat mainly due to its higher RUE_{cycle} ($3.2\,g\,MJ^{-1}$) in comparison to wheat ($2.0\,g\,MJ^{-1}$) as radiation intercepted was similar in each of the growing conditions. In both species and nitrogen rates, water restriction reduced RUE_{cycle} by ca. 20% respect to the fully irrigated treatment (Table 3).

The small differences in radiation interception (and the fact that most of the differences among treatments were due to RUE) could be associated with the fact that LAI reached critical values, maximizing the intercepted radiation, in all cases. Although maximum LAI was ca. 2–3 folds higher than the critical value, the large effects of treatments (irrigated and drought) on LAI did not translate in similar differences in IPAR. In average the light attenuation coefficient (k) was higher in wheat (0.57) than in triticale (0.42) (Table 4). This is why critical LAI was higher in triticale than in wheat (Fig. 5). Water restriction reduced k values ca. 26% respect to irrigated treatment. This coefficient was significantly affected by drought under N_1 in Escudo and Tizne but not in Yagan. Under N_0 the attenuation

Table 2

Intercepted photosynthetically active radiation (IPAR) and radiation use efficiency (RUE) during pre and post-anthesis, for 11 triticale cultivars grown in two regimens of water regimes (I: irrigated; D: drought). Data correspond to the Experiment 1.

Cultivars	$IPAR_{pre-anthesis}$ (MJ m^{-2})		$RUE_{pre-antesis}$ (g MJ^{-1})		$IPAR_{post-anthesis}$ (MJ m^{-2})		$RUE_{post-anthesis}$ (g MJ^{-1})	
	I	D	I	D	I	D	I	D
Remedios	409b[a]	**346**bc[b]	3.2cde	**2.4**a	267bc	224b	5.0a	**2.8**a
Tehuelche	491a	462a	2.9e	2.5a	309abc	**192**b	3.9bc	**2.3**a
Presto	499a	471a	2.7e	2.6a	268bc	**166**b	4.0bc	**1.5**a
Yagan	477a	**438**ab	3.1de	**2.4**a	308abc	**271**ab	4.4ab	**1.7**a
Genú	417b	392ab	4.2ab	**2.2**a	275bc	**347**a	3.3cd	**1.8**a
Quiñe	447ab	**405**ab	4.6a	**2.3**a	283bc	**217**b	2.1e	**2.1**a
Ñinca	450ab	**382**ab	4.4ab	**2.9**a	263c	**200**b	2.2e	2.6a
Tizne	449ab	444ab	3.8bcd	3.4a	289bc	**222**b	3.0d	3.3a
Cerrillo	286c	262cd	3.8bc	**2.6**a	345a	**233**ab	4.0bc	**2.1**a
Boaglio	412b	**369**abc	3.9abc	**3.0**a	269bc	267ab	5.0a	**3.1**a
Maravilla	277c	**231**d	4.2ab	**2.5**a	311ab	**248**ab	3.7bcd	**3.2**a
Mean	419a[c]	382b	3.7a	**2.6**b	290a	235b	3.7a	2.4b

[a] Means within an each water regime followed by the same letter do not differ significantly ($\alpha = 0.05$) with the Tukey test.

[b] Means in bold differ significantly from the values for the same cultivar in the other water regime ($\alpha = 0.05$) with the Tukey test.

[c] Column means followed by the same letter do not differ significantly from those of the other water regime ($\alpha = 0.05$) with the Tukey test.

coefficient was significantly reduced in all cultivars by drought (Table 4).

Differences observed in yield between the two triticales and wheat were mainly explained by differences in the number of grains per unit land area ($r^2 = 0.94$, $P < 0.001$) rather than by variations in AGW ($r^2 = 0.07$ ns). In spite of the differences in yield between triticale and wheat the harvest index in both species was similar, except under N_0 where the harvest index in triticale was lower than in wheat (Table 5), possibly because triticale produced more biomass than wheat. Grain yield in triticale was mainly based on main shoots contribution (ca. 74%), while in wheat both main shoots and tillers contributed similarly, as wheat had a higher number of spikes per unit land area than triticale (Fig. 6). Thus, the higher number of grains per unit land area observed in triticale, when compared to wheat, was mainly associated with a higher number of grains per spike, despite the number of fertile spikelets did fall particularly in triticale when water restrictions were applied (Table 5).
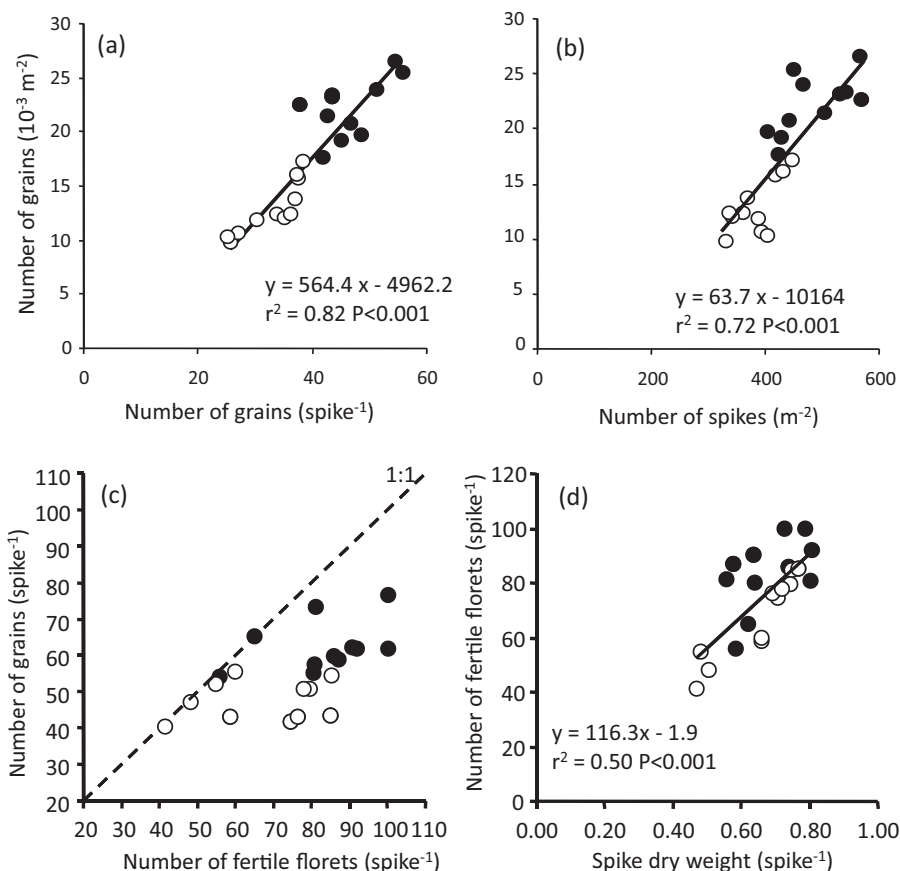

Fig. 4. Relationships between the number of grains per m^2 and its components the number of spikes per m^2 (a) and the number of grains per spike (b) for the whole canopy. To explain differences in grains per spike we related this trait with the number of fertile florets per spike at anthesis (c) and the latter with the spike dry weight at anthesis (d) for main shoots only (we determined florets only in these spikes). In all cases data-points represent the 11 triticale cultivars grown under well irrigated (closed symbols) and drought (open symbols) conditions. Dashed line in panel c represents $y = x$. Data correspond to Experiment 1.

Table 3

Above ground dry matter at physiological maturity ($AGDM_{cycle}$), intercepted photosyntetically active radiation ($IPAR_{cycle}$) and radiation use efficiency (RUE_{cycle}) for two triticale cultivars (Tizne and Yagan) and one wheat (Escudo) grown in two contrasting water regimes (I: irrigated; D: drought) and two nitrogen levels ($N_0 = 115$ and $N_1 = 217$ kgN ha^{-1}). Data correspond to Experiment 2.

Nitrogen	Cultivar	$AGDM_{cycle}$ (g m^{-2})		$IPAR_{cycle}$ (MJ m^{-2})		RUE_{cycle} (g MJ^{-1})	
		I	D	I	D	I	D
N_1	Escudo	2617c[a]	**1688**d[b]	1174a	1178a	2.5c	**1.6**d
	Tizne	4246a	**2732**b	1149a	**1016**b	3.6a	**3.0**a
	Yagan	4200a	**3320**a	1146a	**1002**b	3.7a	**3.2**a
Mean		3687a[c]	2580b	1156a	1065a	3.3a	2.6b
N_0	Escudo	2407d	**1606**d	1178a	**728**d	2.2c	2.1c
	Tizne	3665b	**2232**c	1059b	**801**d	3.4b	**2.8**b
	Yagan	4047b	**2625**b	1051b	**914**c	3.8a	**2.7**b
Mean		3373a	2154c	1096a	814b	3.1b	2.5b

[a] Means within an each water regime followed by the same letter do not differ significantly ($\alpha = 0.05$) with the Tukey test.

[b] Means in bold differ significantly from the values for the same cultivar in the other water regime ($\alpha = 0.05$) with the Tukey test.

[c] Column means followed by the same letter do not differ significantly from those of the other water regime ($\alpha = 0.05$) with the Tukey test.

Table 4

Light attenuation coefficient (k) for two triticale cultivars and one wheat grown under two regimes of water supplied and two nitrogen levels. Data correspond to Experiment 2.

Nitrogen	Cultivar	k	
		I	D
N_1	Escudo	0.68a[a]	**0.59**a[b]
	Tizne	0.46b	**0.35**b
	Yagan	0.50b	0.48a
Mean		0.55a[c]	0.47b
N_0	Escudo	0.67a	**0.34**a
	Tizne	0.51b	**0.32**a
	Yagan	0.45b	**0.34**a
Mean		0.54a	0.33c

[a] Means within an each water regime followed by the same letter do not differ significantly ($\alpha = 0.05$) with the Tukey test.

[b] Means in bold differ significantly from the values for the same cultivar in the other water regime ($\alpha = 0.05$) with the Tukey test.

[c] Column means followed by the same letter do not differ significantly from those of the other water regime ($\alpha = 0.05$) with the Tukey test.

Thus, triticale increased the number of grains per spike associated mainly with the generation of more fertile spikelets and a similar number of fertile florets each (Fig. 7a); so that even with a clear failure of several fertile florets to set grains (that was not evident in wheat) it produced more grains. In turn, the increased number of fertile florets seemed to have been the consequence of a higher availability of resources during floret development as there was a rather strong relationship between the number of fertile florets per spike and the spike dry weight at anthesis (Fig. 7b). Species and cultivar differences were maintained across water regimens. It was interesting to note that the far larger number of spikelets of triticale did not negatively affect the development of florets in each spikelet: it can be seen clearly that both in triticale and in wheat, within each water regime, the development of the 4 floret primordia closest to the rachis was rather similar (Fig. 7c). Interestingly, under both water regimes, they tended to differ in the development of the florets of more distal positions (clearly florets 5 and 6 developed more in triticale than in wheat), although in none of the cases these florets reached the stage of fertile floret at anthesis (Fig. 7c). Drought reduced dramatically the developmental rate of distal florets both in triticale and wheat, but did not affect much the development of the most proximal 3 florets, and therefore there was not a clear effect of the water regime in the number of fertile florets per spikelet (Fig. 7c) the effect of drought being restricted to the number of fertile spikelets per spike and spikes per m^2 (see above).

3.3. Comparison between triticale and wheat in Mediterranean and Monsoonal-type of stress

When simulating a Mediterranean-type of stress both triticales consistently outyielded wheat due differences in RUE driving to differences in biomass (Table 6). IPAR under Mediterranean stress

Table 5

Harvest index, spikes per m^2, number of grains per spike in whole plant and number of spikelets per spike, grains per fertile spikelet in the main shoot (MS) in two triticale and one wheat cultivars grown in irrigated (I) and drought (D) conditions and two nitrogen fertilizer rates ($N_0 = 115$ and $N_1 = 217$ kgN ha^{-1}).

Nitrogen	Cultivars	Harvest index		Spikes per m^2		Number of grains spike^{-1}		Spikelets spike^{-1} (MS)		Grains per fertile spikelet (MS)	
		I	D	I	D	I	D	I	D	I	D
N_1	Escudo	0.27a[a]	0.28a[b]	752.3a	663.0a	29.3c	21.1b	19.3b	18.2b	2.3a	2.2a
	Tizne	0.24b	**0.32**a	498.3a	551.0b	47.0b	52.7a	36.3a	**29.6**a	2.1a	**1.8**b
	Yagan	0.32a	0.29a	504.6b	556.0b	65.7a	**53.4**a	37.3a	**30.3**a	2.3a	**1.9**a
Mean		0.27a[c]	0.29b	585.1a	590.0a	47.3a	42.4a	30.8a	26.1a	2.2a	1.9a
N_0	Escudo	0.35a	0.38a	780.9a	581.0a	28.1c	27.2b	18.4b	**15.1**b	2.2a	2.3a
	Tizne	0.29b	0.31b	565.2b	444.0a	50.2b	**36.7**a	37.0a	**29.3**a	2.1a	**1.8**b
	Yagan	0.26c	0.29c	534.9b	554.0a	46.6b	37.2a	35.0a	**31.3**a	2.1a	**1.9**a
Mean		0.30a	0.32b	627.0a	526.3a	41.6a	33.7b	30.2a	25.2a	2.1a	2.0a

[a] Means within an each water regime followed by the same letter do not differ significantly ($\alpha = 0.05$) with the Tukey test.

[b] Means in bold differ significantly from the values for the same cultivar in the other water regime ($\alpha = 0.05$) with the Tukey test.

[c] Column means followed by the same letter do not differ significantly from those of the other water regime ($\alpha = 0.05$) with the Tukey test.

Table 6
Grain yield and yield components for two triticale and wheat cultivars grown in two water regimes simulating Mediterranean and Monsoonal water stresses.

Water regimes	Cultivars	Grain yield (g m^{-2})	AGDM$_{cycle}$ (g m^{-2})	IPAR$_{cycle}$ (MJ m^{-2})	RUE$_{cycle}$ (g MJ^{-1})	Number of grains m^{-2}	AGW (mg)	Spikes per m^{-2}	Number of grains spike^{-1}	Spikelets spike^{-1} (MS)	Grains per fertile spikelet (MS)
Mediterranean	Escudo	558b[a]	2255c	1145a	2.1b	17158b	32.7ab	733.3a	23.5b	17.0c	2.5a
	Tizne	966a	3910b	979b	4.0a	26828a	34.7ab	596.8ab	46.8a	34.4a	1.8a
	Yagan	1062a	4224a	1069a	3.8a	27798a	39.6a	593.6ab	45.9a	34.1a	2.1a
Mean		862a[b]	3463a	1065a	3.3a	23928a	37.1a	641.2a	38.7a	28.5a	2.1a
Monsoon	Escudo	468b	1532c	866c	1.9b	10772b	43.5a	447.6b	24.4b	17.4c	2.2a
	Tizne	392b	1839b	1172a	1.6c	12647b	36.3ab	542.8b	23.2b	25.8b	1.8a
	Yagan	883a	2971a	1012b	2.9a	24456a	31.5b	488.8b	50.8a	29.9b	2.1a
Mean		581b	2114b	1017a	2.1b	15958b	35.7a	493.1b	32.9a	24.4b	2.0a

MS: main shoot.

[a] Means with the same letter comparing cultivars within water regimes are not significantly different ($\alpha = 0.05$) with the Tukey test.

[b] Means with the same letter averaging across cultivars in each water regime are not significantly different ($\alpha = 0.05$) with the Tukey test.

was similar in both species, however, when crops were grown under Monsoonal-type of stress; triticale intercepted 21% more radiation than wheat (Table 6). When crops grown under Monsoonal conditions RUE$_{cycle}$ decreased 36%, respect to that registered in Mediterranean environments, however, the variation between both environments was higher in both triticales than in wheat. In fact RUE$_{cycle}$ under Monsoonal environments dropped 42 and 10%

in triticale and wheat, respectively, in relation to the crop grown under Mediterranean conditions.

Differences in grain yield between triticale and wheat in a Mediterranean-type of stress were due to a higher number of grains per m^2, in turn related to more grains per spike (Table 6). On the other hand, with simulated Monsoonal-type of stress, the triticale cultivar Tizne showed an important reduction in yield, ending up
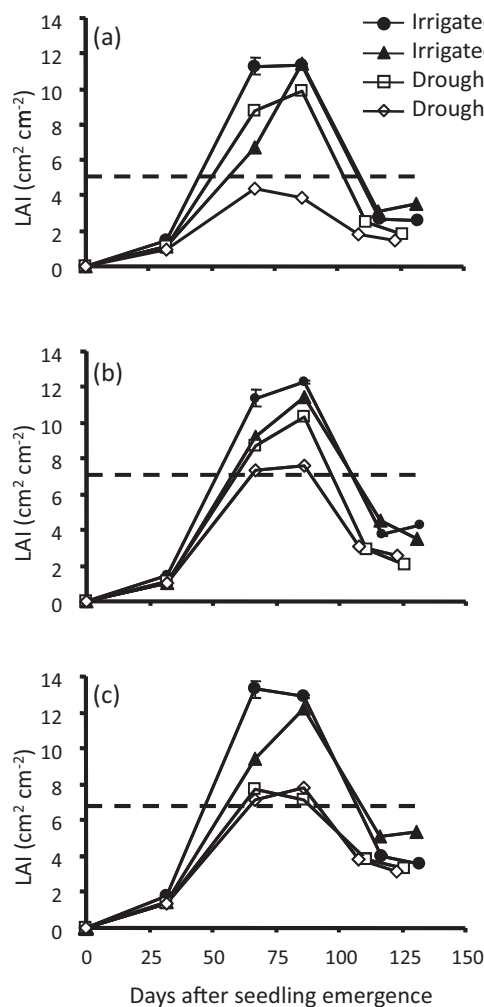

Fig. 5. Leaf area index (LAI) through the crop cycle for Escudo (a), Tizne (b) and Yagan (c). Dashed horizontal line indicates critical LAI. Data correspond to Experiment 2. Bars indicate ± standard error for the mean.
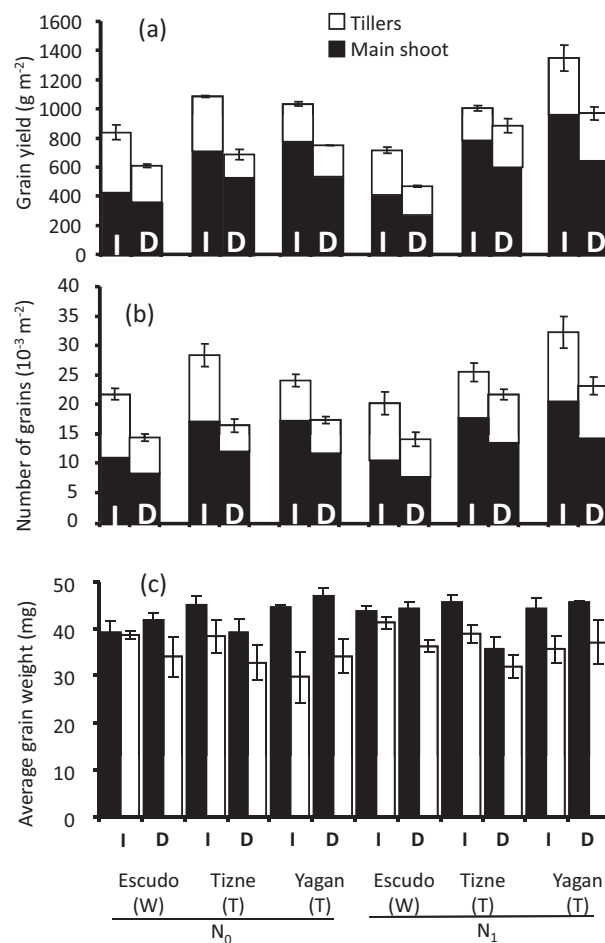

Fig. 6. Grain yield (a), number of grains (b) and average grain weight (c) for two triticale and a wheat cultivars grown under well irrigated (I) and under drought (D) and two nitrogen fertilizer rates (N$_0$ = 115 and N$_1$ = 217 kgN ha^{-1}). Closed bars are main shoots and empty bars tillers. Segments on top of each bar correspond to the standard error. (W = wheat, T = triticale). Data correspond to Experiment 2.
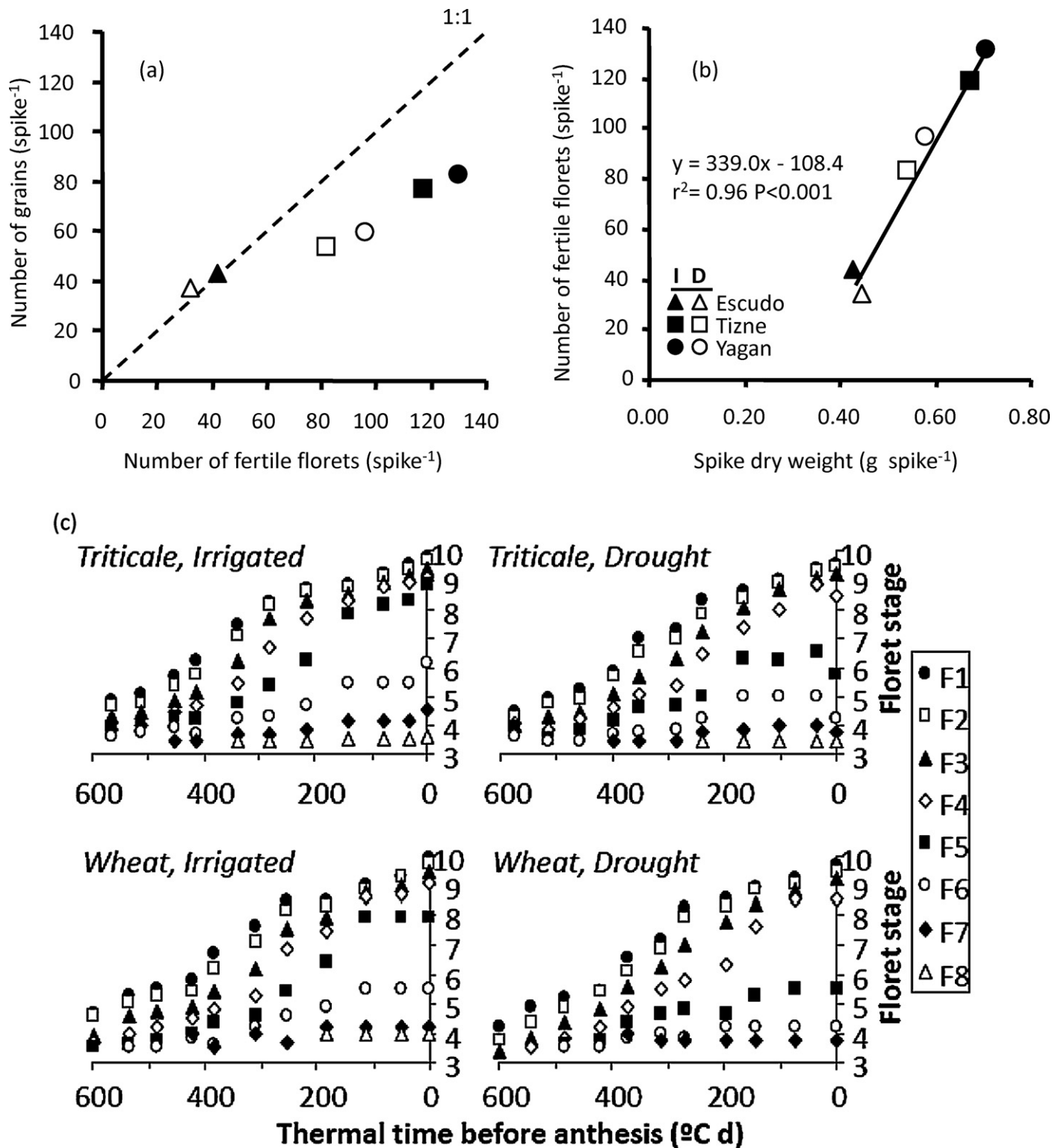
Fig. 7. Relationships between the number of grains per spike at maturity and the number of fertile florets per spike at anthesis (a), and between the number of fertile florets per spike and the spike dry weight at anthesis (b), for two triticale and one wheat cultivars grown under well irrigated (closed symbols) and under drought (open symbols). Dotted line in panel a is the line with intercept zero and slope 1. Panel c shows the patterns of development of floret primordia (from floret 1 [F1] to floret 8 [F8] within a spikelet (numbered from the rachis to more distal positions) during the period immediately preceding anthesis in triticale (average of the two genotypes; top sub-panels) and wheat (bottom sub-panels), either in well irrigated (left sub-panels) or under drought conditions (right sub-panels). Data correspond to Experiment 2.

with similar yield to that of wheat (Table 6). Once again the number of grains per unit land area explained most of the differences in yield. The AGW under Mediterranean conditions was similar in both species, but when crops were grown under Monsoonal-type of environment; the grains in wheat were heavier (22%) than in triticale (Table 6).

4. Discussion

The results of this study showed a great variation in grain yield, biomass production and its physiological components among triticale cultivars when grown under contrasting water conditions. In general, variations in yield were explained by changes in the number of grains per unit land area more than by variations in grain weight. This is in line (i) with previous evidences in triticale reinforcing the importance of number of grains on grain yield (Ford et al., 1984; Giunta et al., 1999; Santiveri et al., 2004) and (ii) with the concept that yield in cereals is far more limited by sink strength than by assimilate availability during grain filling (e.g. Borrás et al., 2004; Slafer et al., 2005). Drought reduced AGDM, more than its partitioning to the reproductive organs (Sutton and Dubbelde, 1980; Giunta et al., 1993; Lopez-Castañeda and Richards, 1994), mainly through reduced RUE. The larger impact on RUE, more than in $IPAR_{cycle}$, could be attributed to the high values of LAI (much higher than the critical LAI maximizing light interception) achieved in the study so that, reductions in this traits by drought may have had only marginal effects on the ability of the canopy of intercept radiation. Although LAIs found in the present study were high, they were similar to maximum values reported elsewhere (Goyne et al., 1993; Calderini et al., 1997; Miralles and Slafer, 1997). In line with what was found in this study, Muchow (1989) and Jamieson et al. (1995) found that RUE was more affected by water stress than IPAR. It was shown that water stress affected light interception or RUE depending on the timing of water stress in relation to the canopy development (Thomas and Fukai, 1995; Giunta and Motzo, 2004).

RUE has been suggested to be a stable attribute of the crop for particular species and under non-stressed conditions (Monteith, 1977; Wilson and Jamieson, 1984; Kiniry et al., 1989). However, the results of this study showed that, for a wide range of triticale cultivars, RUE was largely variable independently of the environment. On the other hand, the triticale cultivars differed largely in phenology (see Estrada-Campuzano et al., 2008), and that would be a possible explanation, at least in part, of the variation in RUE observed in this study. Variability in RUE was also reported by Gregory et al. (1992) and Goyne et al. (1993) for barley, and by Calderini et al. (1997), Miralles and Slafer (1997) and Muurinen and Peltonen-Sainio (2006) for wheat. A striking feature of our results was that for some cultivars the estimated RUE in postanthesis was greater than in pre-anthesis, probably due to the methodology used to measure IPAR (and calculated RUE) after anthesis. By trying to avoid the layer of senesced leaves when estimating radiation interception the sensor was placed slightly above of the layer of senesced leaves which might have induced to an underestimation of postanthesis IPAR and consequently an overestimation of RUE during this period of net leaf senescence. Muurinen and Peltonen-Sainio (2006) also measured transmitted radiation placing the linear sensor just above the yellowing leaves and have faced similar likely overestimation of RUE during post-anthesis.

The close and significant relationship between CGR_{cycle} and RUE_{cycle}, observed in this study, revealed that the reductions in biomass production by effect of water stress were mainly due to reductions in crop growth rate as a consequence of low efficiency of the crop to transform the intercepted radiation into biomass (Fig. 8). Similar results were found by Jamieson et al. (1995) and
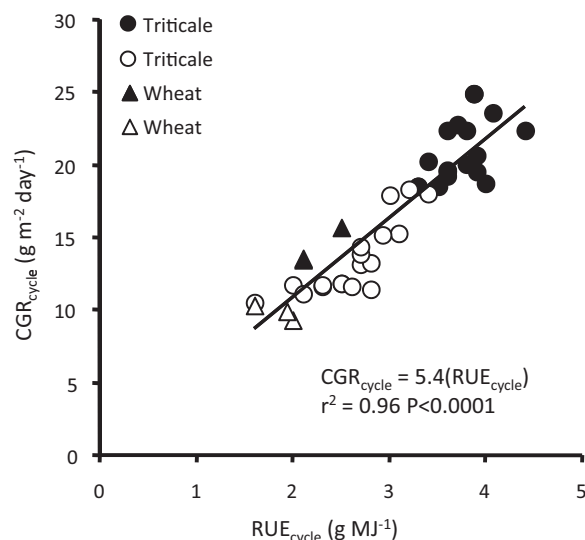
Fig. 8. Relationship between crop growth rate (CGR_{cycle}) and radiation use efficiency (RUE_{cycle}) during the crop cycle for different triticale cultivars (circles) and wheat (triangles) grown in irrigated (closed symbols) and drought (open symbols) conditions. Data corresponding to the three experiments.

Thomas and Fukai (1995) who observed that water stress reduced crop growth rate mainly through its effect on RUE.

When both species wheat and triticale with the same duration to anthesis were compared, the results of this study showed that triticale outyielded wheat independently of water and nitrogen conditions. The better performance of triticale was mainly due to an increased biomass at anthesis and at maturity in line with previous evidences (Sutton and Dubbelde, 1980; Lopez-Castañeda and Richards, 1994; Royo and Tribó, 1997). The higher biomass production of triticale respect to wheat, and in coincidence with what was observed in Experiment 1 when different triticale cultivars were compared, was mainly associated with higher RUE more than by differences in IPAR. The higher RUE in triticale respect to wheat could be due to its lower coefficient of light attenuation allowing a better light distribution through canopy (Green, 1989; Miralles and Slafer, 1997; Muurinen and Peltonen-Sainio, 2006). Thus, triticale advantages were especially noticeable in the Mediterranean-type environment where yield and biomass were almost two-fold those of wheat, associated with differences of similar magnitude in RUE. The superiority of triticale respect to wheat in Mediterranean environments is in line with the evidences shown by Sutton and Dubbelde (1980), Sweeney et al. (1992), and Lopez-Castañeda and Richards (1994). When the drought was imposed before anthesis (i.e. Monsoonal-type of environment) the differences in grain yield and AGDM were explained not only by RUE but also by IPAR, as early water stress affected LAI. This agrees with results from Giunta and Motzo (2004), who found that when the stress occurred early in the cycle both IPAR and RUE were affected, while RUE was reduced when water stress occurred later in the cycle. The RUE in wheat cultivar was very stable in both Mediterranean- and Monsoon-type environments indicating that when the stress is imposed early in the crop cycle triticale seems more responsive than wheat.

Triticale outyielded wheat in all environments due to its constitutive higher number of grains m^{-2}, as result of a higher number of grains spike^{-1}. This agrees with previous evidences reporting yield advantages of triticale under dry environments respect to wheat due to a greater grain number m^{-2} (Ford et al., 1984; Giunta et al., 1993; Giunta and Motzo, 2005) and grains per spike (Giunta et al., 1993; Lopez-Castañeda and Richards, 1994; Giunta and Motzo, 2005). Also the fact that most of yield in triticale is produced in main

shoots, while in wheat main shoots and tillers contribute more similarly to crop yield, is also in line with what was observed by others (Sutton and Dubbelde, 1980; Ford et al., 1984; Sweeney et al., 1992; Lopez-Castañeda and Richards, 1994).

The fact that differences in grains per spike were related to parallel differences in spikelets per spike indicates that in triticale the effect of having florets simultaneously developing in more spikelets than wheat did not represent any significant reduction in the rates of floret development. This might have been associated with the fact that spike dry weight was also heavier in triticale than in wheat. In fact dividing the spike dry weight per the number of spikelets per spike resulted in similar values of "dry matter per spikelet" in wheat and triticale, which is consistent with the idea that floret development within spikelets might be associated with the availability of resources (González et al., 2011 and previous references quoted therein).

Similarly to what was demonstrated in wheat (Fischer, 1985; Miralles et al., 2000; González et al., 2005a,b; Slafer, 2003) and barley (Arisnabarreta and Miralles, 2008), the acquisition of dry matter by the spike during floret development just before anthesis seemed critical for the survival of floret primordia, as evidenced by the strong relationship between the number of fertile florets and spike dry weight at anthesis. Even though there were a clearly higher proportion of fertile florets that failed in setting grains in triticale than in wheat, the increased number of fertile florets was critical to produce more grains per m^2. The higher abortion (fertile florets not producing mature grains) may not be a constitutive characteristic of triticale but just an indirect consequence of its constitutively higher number of fertile florets per spike. This would be in agreement with what was reported by González et al. (2005a) in wheat, who found that the proportion of fertile florets not setting grains was increased together with the increase in the number of fertile florets.

Summarizing, water deficit significantly affected biomass production in triticale mainly due to reductions in RUE. Additionally, the reductions in grain yield by the effect of water stress were better explained by reductions in total biomass more than by changes in harvest index. Grain weight seemed to be a more conservative trait as water deficit affected more the number of grains than grain weight. In fact, the variations in grain yield due to changes in water availability were associated more with change in grains per unit area than in grain weight. Regardless of environmental conditions triticale produced more biomass than wheat mainly due to greater RUE.

Acknowledgements

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