Euphytica (2005) 146: 203–212
DOI: 10.1007/s10681-005-9006-2

Yield Formation in Mediterranean durum wheats under two contrasting water regimes based on path-coefficient analysis

L.F. García del Moral[1,*], Y. Rharrabti[1], S. Elhani[2], V. Martos[1] & C. Royo[3]
[1]*Dpto. Fisiología Vegetal, Facultad de Ciencias, Instituto de Biotecnología, Universidad de Granada, 18071–Granada, Spain;* [2]*University of Quebec in Chicoutimi, Chicoutimi, Quebec, Canada;* [3]*Centre UdL-IRTA, Area de Conreus Extensius, Rovira Roure, 191, 25198–Lleida, Spain (*author for correspondence: e-mail: lfgm@ugr.es)*

Received 17 February 2005; accepted 31 August 2005

Key words: durum wheat, mediterranean environment, path-coefficient analysis, yield formation

Summary

The components of grain yield are altered by adverse growing conditions as the effects of certain environmental factors on crop growth and yield differ depending upon the developmental stages when these conditions occur. Path-coefficient analysis was used to investigate the main processes influencing grain yield and its formation under Mediterranean conditions. Twenty-five durum wheat genotypes, consisting of four Spanish commercial varieties and 21 inbred lines from the ICARDA durum wheat breeding program, were grown during 1997 and 1998 under both rainfed and irrigated conditions in southern Spain. Path-coefficient analysis revealed that under favourable conditions grain yield depended in equal proportion on the three primary yield components (i.e. spikes m^{-2}, grains $spike^{-1}$, and mean grain weight), whereas in the rainfed experiments, variations in grain yield were due mainly to spikes m^{-2} and to a lesser extent to grains $spike^{-1}$. Compensatory effects were almost absent under irrigated treatments; however, under water shortage, spikes m^{-2} exerted a negative influence on grain $spike^{-1}$ due mainly to a negative interrelationship between tiller production and apical development. These compensatory effects could partially explain the restricted success in durum wheat breeding observed in water-limited environments of the Mediterranean region. Under rainfed conditions the number of spikes m^{-2} depended mainly on the ability for tiller production, whereas in the irrigated experiments the final number of spikes was determined mostly by tiller survival.

Introduction

Grain yield in small-cereals can be analysed in terms of three primary yield components (number of spikes m^{-2}, number of grains $spike^{-1}$ and mean grain weight) that appear sequentially with later-developing components under the control of earlier-developing ones (Hamid & Grafius, 1978; Garcia del Moral et al., 1991; Simane et al., 1993). In the Mediterranean region, the magnitude attained by these yield components could be limited by low and unpredictable seasonal rainfall as well as higher temperatures towards the end of the crop cycle. In this region, most rain falls during autumn and winter, and water deficit occurs in the spring, resulting in moderate stress for rainfed wheat around anthesis, which increases in severity throughout grain filling (Edmeades et al., 1989). Therefore, it appears necessary to study the physiology of crop development, as the effects of certain environmental factors on crop growth and yield differ depending upon the developmental stages when these factors act. In other words, grain yield is more sensitive during certain developmental phases than others to adverse growing conditions (Landes & Porter, 1989; Slafer et al., 1996; Garcia del Moral et al., 2002).

Tillering, as one of the first developmental processes in wheat, depends mainly on the availability of water and nitrogen (Simons, 1982; Simane et al., 1993). Tiller death may occur prior to anthesis and is accentuated particularly under mid-season drought stress (Simons, 1982). During rapid vegetative growth, floral primordia develop and thus floral and vegetative organs may compete for limiting resources (Miralles et al., 2000). This in turn can lead to a higher rate of floral mortality, reducing thus the final number of fertile florets, particularly under drought conditions typical of the Mediterranean environment (Miralles et al., 2002). At the end of the plant cycle, grain filling is maintained by a high contribution from assimilation before and immediately after anthesis and remobilization of vegetative reserves during kernel growth, especially under water shortage (Bidinger et al., 1977; Royo et al., 1999).

A considerable number of studies in small-grain cereals include correlations between grain yield and its related characters. Although these are helpful in determining the principal components influencing final grain yield, they provide incomplete information on the relative importance of the direct and indirect effects on the individual factors involved. These considerations are practically observed in wheat, where yield components occur successively and may, therefore, interact in compensatory patterns during plant development (Simane et al., 1993; Gibson & Paulsen, 1999). Thus, simple correlations may not provide a clear picture of the importance of each component in determining grain yield. Path-coefficient analysis divides the correlation coefficients into direct and indirect effects. It allows the separation of the direct influence of each yield component on grain yield from the indirect effects caused by the mutual relationships among yield components themselves. Although literature is abundant on the use of path-coefficient analysis to investigate the relationships between grain yield and yield components in cereals, little information is available on the use of this technique to evaluate the formation of yield components in relation to the water regime and its influence on grain-yield variations, especially under Mediterranean environmental conditions.

Thus, the objectives of this work were: (i) to evaluate the effects of water availability on several traits determining the development of yield components in durum wheat and its influence on grain yield, and (ii) to use path-coefficient analysis to investigate the main developmental processes influencing grain-yield formation under Mediterranean conditions. Although some previous studies have examined yield formation in durum wheat under Mediterranean conditions using path analysis (Simane et al., 1993), this study is novel in that a path diagram is proposed that reveals not only the influence of yield components on grain yield, but also analyses the process that determines the formation of these yield components. This gives a more complete view of how water availability affects grain-yield formation in durum wheat in Mediterranean environments.

Materials and methods

Experimental design

Four field trials were conducted during 1997 and 1998 in two contrasting environments (under irrigated and rainfed conditions) in the province of Granada (south-eastern Spain) characterized by a continental Mediterranean climate with adequate rainfall during winter (December and January), limited rainfall during late spring (mid–April to mid–May), and sparse rainfall during February and March. Sowing dates, the normal in the zone, coincided with significant rainfall events in each year. Soil characteristics, sowing dates and agronomical practices are summarized in Table 1.

To evaluate the variability existing among durum wheat germplasm in the Mediterranean area, 21 inbred lines from the ICARDA durum wheat-breeding program and four of the most cultivated Spanish commercial cultivars were selected (Table 2).

In each trial, genotypes were sown in a randomized complete-block design with 4 replications. The seeding rate was adjusted to a density of 350 viable seeds m^{-2}. Plot size was 12 m^2 (6 rows, 20 cm apart).

Components of yield formation

The length of vegetative period was calculated as days from sowing to anthesis (growth stage 65 according to Zadoks et al., 1974). Grain-filling duration was considered to be the days from anthesis to physiological maturity (growth stage 91). Number of tillers was measured by counting tillers in 1 m of one of the central rows in each plot at the end of tillering, anthesis and harvest. For the last sampling, total spikes per m^{-2} were counted and spikelets $spike^{-1}$ and grains $spike^{-1}$ were determined in a sub-sample of 10 selected plants. The number of grains $spikelet^{-1}$ was then calculated by dividing the number of grains $spike^{-1}$ by the number of spikelets $spike^{-1}$. Mean grain weight was calculated from the weight of three sets of 300 grains per plot. Tiller survival was calculated by dividing the tiller number at harvest by the maximum tiller number at the end of tillering, expressed as a percentage.

Table 1. Site localization and agronomical details

Environment				
Water regime	Irrigated		Rainfed	
Coordinates	37°21′N 03°35′W		37°10′N 03°50′W	
Soil characteristics:				
Classification	Typic Xerofluvent		Loamy Calcixerolic Xerochrept	
Texture	Silty clay		Silty clay	
pH	8.0		8.2	
P (ppm)[a]	50		27	
K (ppm)[b]	88		210	
Organic matter (%)	2.01		1.86	
Year	1997	1998	1997	1998
Seasonal rainfall[c] + irrigation (mm)	197+150	311+150	184	288
Average temperatures during grain-filling period				
T_{max}	23.9	26.0	23.6	28.9
T_{mean}	16.4	19.2	17.4	21.3
T_{min}	8.8	12.4	11.1	13.8
Agronomic practices:				
Fertilizers				
Type	Complex 15 15 15			
Nitrogen at seed bed	10% as NH_4NO_3 + 5% as urea			
Nitrogen at top dressing	Ammonium nitro sulphate 26%			
Phosphorus	15% as $Ca(H_2PO4)_2$			
Potassium	15% as K_2SO_4			
(kg ha^{-1})				
N (seed bed + top dressing)	60+60	60+20	45+20	45+20
P_2O_5	60	60	45	45
K_2O	60	60	45	45
Sowing dates	05/01/97	11/12/97	13/01/97	12/12/97

[a]Extracted following the Bray II method.
[b]Extraction with neutral 1 M ammonium acetate.
[c]I.e, from sowing to harvesting.

For measuring grain growth, 100 main spikes were tagged at anthesis in each plot. Five randomly tagged spikes were removed twice per week from anthesis to ripening, and six grains were taken from the central spikelets of each spike. The grains were oven dried at 70 °C for 48 h to determine dry weight. The grain-filling rate was determined as the slope of the linear regression of grain dry-weight against time. Grain yield was determined on the basis of the harvested plot in all trials and corrected to a 12% moisture basis.

Statistical and path-coefficient analyses

Combined analyses of variance for grain yield, primary yield components (spikes m^{-2}, grains spike^{-1}, and mean grain weight), secondary yield components (maximum tiller number at the end of tillering, tiller survival, spikelets spike^{-1}, and grains spikelet^{-1}) and developmental traits (vegetative period, grain-filling duration and grain-filling rate) were performed over trials after verifying the homogeneity of trial variance errors using Bartlett's test. Years and replications (blocks) were considered random factors and the remainder fixed. Least significant difference (LSD) values were calculated at the 5% probability level. The SAS (SAS Institute, Inc., 1997) procedures and programs were used for these calculations.

After computing the correlation coefficients between all characters, path-coefficient analysis were performed using a combination of the methods described by García del Moral et al. (1991) and Dofing & Knight (1992). Before computing the path coefficients, data

Table 2. Origin, pedigree, characteristics and grain yield of the genotypes used

Genotype	Origin	Pedigree	Characteristics	Grain yield (kg ha^{-1})
Altar-aos	Spain	Altar × Aos	High yield, recently introduced	2782
Awalbit	ICARDA	ICD81-0322-ABL-5AP-TR-AP-6AP-0TR	Low canopy temperature	2622
Bicrecham-1	ICARDA	ICD87-0459-0TR-ABL-AP0TR-4AP-0AP	High yield,	3167
Chacan	ICARDA	ICD88-1104-ABL-0TR-5AP-AP-3AP-0AP	Low chlorophyll content	2660
Chahra-1	ICARDA	CD27672-4AP-3AP-0AP	High chlorophyll content	2773
Haurani	ICARDA	Hauran selection	Old check, low yield potential	1849
Jabato	Spain	closed	Commercial, good adaptation to Andalusia region	3289
Korifla	ICARDA	CD523-3Y-1Y-2M-0Y-0AP	Intensively used in SEWANA for scientific research	2793
Krs/Haucan	ICARDA	ICD88-1400-ABL-4AP-0AP-3AP-0AP	Low carbon isotope discrimination	2741
Lagost-3	ICARDA	ICD89-0471-ABL-0TR-8AP-0TR-25AP-0TR	Resistance to high temperatures	2638
Lahn/Haucan	ICARDA	CD20626-1AP-2AP-1AP-0KE–0AP	Resistance to high temperatures	2852
Massara-1	ICARDA	Mrb3/4/BYE*2/Tc//ZB/W/3/Cit	ICARDA check	2699
Moulchahba-1	ICARDA	ICD89-0264-AL-4AP-0AP-1AP-0AP	Low carbon isotope discrimination	2799
Mousabil-2	ICARDA	ICD89-0263-AL-4AP-0AP-5AP-0AP	High yield, high carbon isotope discrimination	2834
Omlahn-3	ICARDA	ICD85-0642-ABL-28AP-0TR-AP-0TR	High yield, high chlorophyll content	2978
Omrabi-3	ICARDA	L0589-4L-2AP-3AP-0AP	Resistance to high temperatures, low carbon discrimination	2876
Omruf-3	ICARDA	ICD86-0436-ABL-0TR-3AP-0TR	Low canopy temperature	2899
Quadalete/Erp/Mal	ICARDA	ICD87-0993-ABL-1AP-0TR-7AP-0TR	High tillering capacity	2648
Sebah	ICARDA	ICD86-0041-ABL-13AP-0TR-7AP-0TR	High mean grain weight	2505
Mexa	Spain	GDOVZ469/3/Jo's//61130/LSL	Very cultivated in Spain, Earliness	2492
Stojocri-3	ICARDA	ICD83-0050-3AP-4AP-0TR-1AP-0TR		2452
Vitrón	Spain	Yavaro's'	Widely grown cultivar from Spain	2938
Waha	ICARDA	Cham 1 : Plc/Ruff//Gta/Rtte	Cold sensitive, high carbon discrimination, ICARDA check	3061
Zeina-1	ICARDA	ICD88-1233-ABL-0TR-4AP-0AP-1AP-0AP	Low chlorophyll content	3042
Zeina-2	ICARDA	ICD88-1233-ABL-8AP-0AP-3AP-0AP	Low chlorophyll content	2951

were transformed to decimal logarithms in order to convert the relationships between variables from multiplicative to additive, and subsequently standardize them (García del Moral et al., 1991).

Results and discussion

Effect of water stress on grain yield and its related characters

The results from the combined analysis of variance (Tables 3 and 4) show that grain yield and the number of spikes m^{-2}, maximum tiller number at the end of tillering, tiller survival and number of spikelets spike^{-1} were largely influenced by the environment and to a lesser degree by the year. Variations in the number of grains spike^{-1}, mean grain weight, number of grains spikelet^{-1}, and grain-filling rate were caused mainly by the environment × year interaction, whereas phenology were affected primarily by year-to-year variation, although not significantly. Genotype and its interaction effects were of small magnitude, although highly significant.

The effects of water availability on grain yield, primary yield components, and the vegetative and grain-filling periods are displayed in Table 5. There was a general reduction in all characters due to the negative effect that water constraint under rainfed conditions had on yield components from tillering to grain maturity. The effect of water restriction under rainfed conditions was more marked on the number of spikes m^{-2} and

Table 3. Mean squares from the combined analysis of variance of grain yield, primary yield components and vegetative and grain-filling periods of 25 durum wheat genotypes grown during two years (1997 and 1998) in two contrasting environments (irrigated and rainfed)

Source of variation	df	Grain yield ($\times 10^5$) (kg ha^{-1})	Spikes m^{-2} ($\times 10^3$)	Grains spike^{-1}	Mean grain weight (mg)	Vegetative period (days)	Grain-filling period (days)
Env† (E)	1	2374.8***	428.0***	2569.1***	69.9***	4275.9***	2627.4***
Year (Y)	1	955.3	155.7	428.2	1071.0	135104.5	8249.6
E × Y	1	600.7***	12.4	5198.1***	2945.4***	4541.5***	504.5***
Gen (G)†	24	12.7***	14.2***	99.6***	155.3***	15.9***	89.1***
G × E	24	4.6**	9.6***	36.8***	20.0***	16.2***	36.6***
G × Y	24	7.1	11.8	34.6	23.3	22.2**	0.5
G × E × Y	24	7.2***	8.4***	52.0***	13.5***	7.5***	0.6
Block (E × Y)	12	24.7***	16.4***	29.5	10.7**	4.9**	24.5***
Error	288	2.2	3.1	17.4	3.7	1.9	2.8
Total	399						

†Env, environment; Gen, genotype.
*,**,***Significant at 0.05, 0.01 and 0.001 of probability level.

Table 4. Mean squares from the combined analysis of variance of secondary yield components of 25 durum wheat genotypes grown during two years (1997 and 1998) in two contrasting environments (irrigated and rainfed)

Source of variation	df	Maximum tiller number ($\times 10^4$) ($n^\circ \cdot$ m^{-2})	Tiller survival ($\times 10^2$) (%)	Spikelets spike^{-1}	Grains spikelet^{-1}	Grain-filling rate (mg day^{-1})
Env† (E)	1	2274.9***	1123.9***	698.1***	0.12	0.43***
Year† (Y)	1	70.0	66.0	638.3	7.55	3.50
E × Y	1	97.1**	119.9***	390.5***	11.92***	10.67***
Gen (G)	24	6.4***	3.4	4.8***	0.42***	0.36***
G × E	24	5.4***	2.5***	2.6**	0.14*	0.05**
G × Y	24	7.4	2.6	2.1	0.11	0.08*
G × E × Y	24	6.5***	2.2***	2.7**	0.21***	0.04
Block (E × Y)	12	3.4**	2.5***	6.1***	0.12	0.04
Error	288	1.5	0.8	1.3	0.07	0.03
Total	399					

†Env, environment; Gen, genotype.
*,**,***Significant at 0.05, 0.01 and 0.001 of probability level.

Table 5. Mean values of grain yield, primary yield components and vegetative and grain-filling periods of 25 durum wheat genotypes grown during two years (1997 and 1998) in two contrasting environments (irrigated and rainfed)

Environment	Grain yield (kg ha^{-1})	Spikes m^{-2}	Grains spike^{-1}	Mean grain weight (mg)	Vegetative period (days)	Grain-filling period (days)
Irrigated	3544	512	27.6	42.0	113.9	29.8
Rainfed	2003	446	22.5	41.2	107.4	24.7
% decrease	43.5	12.9	18.5	1.9	5.7	17.1
Lsd†	92	11	0.8	0.4	0.3	0.3

The percentage of decrease caused by drought is also shown.
†Least significant difference at $P = 0.05$.

Table 6. Mean values of secondary yield components of 25 durum wheat genotypes grown during two years (1997 and 1998) in two contrasting environments (irrigated and rainfed)

Environment	Maximum tiller number ($n^\circ \cdot m^{-2}$)	Tiller survival† (%)	Spikelets spike^{-1}	Grains spikelet^{-1}	Grain-filling rate (mg day^{-1})
Irrigated	1006	53.0	13.7	2.05	1.83
Rainfed	529	86.6	11.1	2.02	1.77
% decrease	47.4	–	19.0	1.5	3.3
Lsd‡	24	1.8	0.2	0.05	0.03

The percentage of decrease caused by drought is also shown.
†Percentage of reduction caused by high tiller production in the irrigated environment.
‡Least significant difference at $P = 0.05$.

grains spike^{-1}, traits that develop during the period most sensitive to drought occurrence, i.e., from double ridge to anthesis (Shpiler & Blum, 1991). Giunta et al. (1993) also reported that severe water deficit around anthesis seriously influences wheat yield, reducing the number of spikes and spikelets and, therefore, decreasing plant fertility. Mean grain weight was less affected by water shortage under rainfed conditions, appearing as a relatively stable trait, possibly due to the high proportion of translocated pre-anthesis reserves for grain filling when the photosynthetic source is limited by stress (Bidinger et al., 1977; Blum, 1983; Blum et al., 1994). The plant cycle was also shortened under rainfed conditions, mainly as a consequence of higher temperatures. This effect was attenuated in the irrigated site, probably due to the abundance of water to the plant during the critical phases of development (i.e., tillering and grain growth).

Increasing tillering ultimately reduced tiller survival, probably due to competition for water and nutrients, which was more pronounced under Mediterranean conditions as tiller proliferation augments. High soil moisture and fertility of the irrigated site favoured a high tiller number (Table 6), but with a low percentage of survival. In contrast, tiller production was reduced under rainfed conditions, favouring their survival (Table 6), and thus the number of tillers present at the end of tillering was more important in determining the final spike density. Similar observations have been reported in other works on wheat (Davidson & Chevalier, 1990) and barley (García del Moral & García del Moral, 1995).

Interrelationships between the characters studied

The results of the path-coefficient analysis corresponding to the irrigated and rainfed sites are shown in the diagram of the Figures 1 and 2, respectively. This path diagram demonstrates the influence of yield components on grain yield as well as the processes that determined the magnitude of these yield components, thereby providing a more complete view of how rainfed and irrigated conditions affect grain-yield formation in durum wheat under Mediterranean environments.

Vegetative period and the maximum tiller number are assumed to have a mutual relationship (correlation coefficient) because both parameters may exercise a reciprocal influence during the early crop development. In the same way, rate and duration of grain filling are shown to interact reciprocally during the grain-growth period.

Grain yield in the irrigated site (Figure 1) depended at an equal proportion on the three primary yield components (spikes m^{-2}, grains spike^{-1} and mean grain weight). However, under rainfed conditions, variations in grain yield were caused largely by spikes m^{-2} and to a lesser extent by grains spike^{-1} (Figure 2). Under these conditions, the mean grain weight exerted no significant direct influence on grain yield. The number of spikelets spike^{-1} had a significant direct effect on grain yield only at the irrigated site (Figure 1), while the fertility of spikelets did not exercise a direct significant influence on grain yield under either treatment.

The number of spikes m^{-2} had no significant effect on the number of grain spikes^{-1} or mean grain weight in the irrigated treatment (Figure 1), probably due to a sufficient amount of water and nitrogen, accompanied by moderate temperatures during the growing season. In the rainfed environment, however, a high number of spikes m^{-2} was associated with fewer grains spike^{-1}, but without a significant effect on mean grain weight (Figure 2). This agrees with results of Simane et al., (1993) in durum wheat and may well indicate a compensatory effect between tiller production

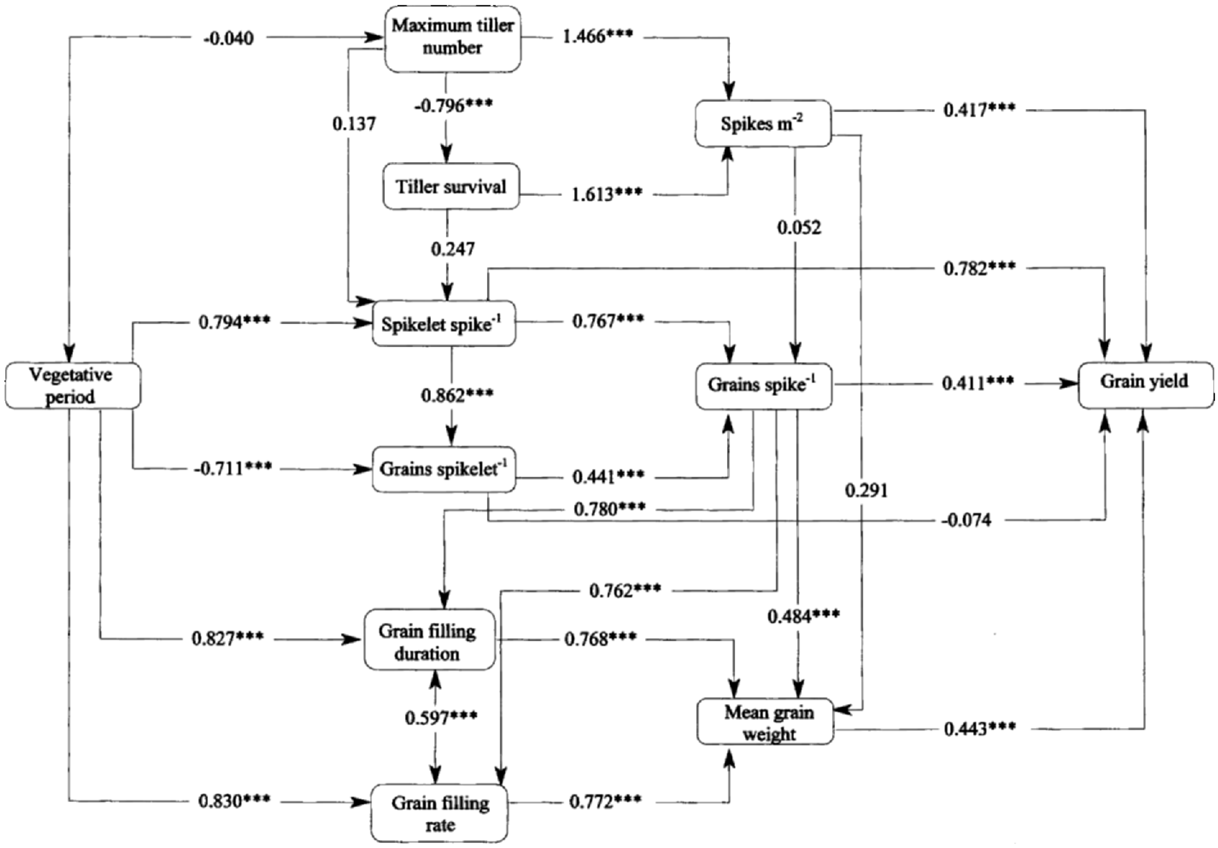

Figure 1. Path-coefficient diagram showing the interrelationships between grain yield, its primary and secondary yield components and the vegetative and grain-filling periods of 25 durum wheat genotypes grown under irrigated conditions during two years (1997 and 1998). The single-headed arrows indicate path coefficients and the double-headed arrows indicate simple correlation coefficients. ***Significant at 0.001 probability level.

and apical development in wheat, presumably deriving from the negative allometry between these traits during plant development (Miralles & Slafer, 1999). Under more favourable conditions of the irrigated treatments, the number of grains spike^{-1} positively influenced mean grain weight, whereas, in the rainfed experiments, final grain weight was not related to grains spike^{-1}.

From the analysis of the secondary yield components, it can be deduced that, under irrigated conditions (Figure 1), the number of spikes m^{-2} depended more on the proportion of tillers that survive to form a spike than on the number of tillers produced at the end of tillering, although both traits significantly influenced the variations of final spike number. However, under rainfed conditions, spike m^{-2} appears to be more influenced by the ability to produce tillers than on their survival (Figure 2), although both direct effects were significant.

The number of grains spike^{-1} depended more on the number of spikelets spike^{-1} than on spikelet fertility under favourable conditions of the irrigated site (Figure 1), whereas in the rainfed environment, the number of grains spikelet^{-1} was the factor that most influenced the number of grains spike^{-1} (Figure 2). Moreover, at the irrigated site, spikes with high numbers of spikelets tended to have more fertility, whereas in the contrasting environment, this relationship was not significant. The number of spikelets spike^{-1} was influenced negatively both by the number of tillers at the end of tillering and the percentage of tiller survival only under rainfed conditions, probably because of a high demand for nutrients between tiller proliferation was detrimental until spikelet differentiation. Under irrigated conditions, however, these relationships were not significant. Experiments that favour high assimilation and translocation during floret development have been shown to increase the number of grains spike^{-1} in

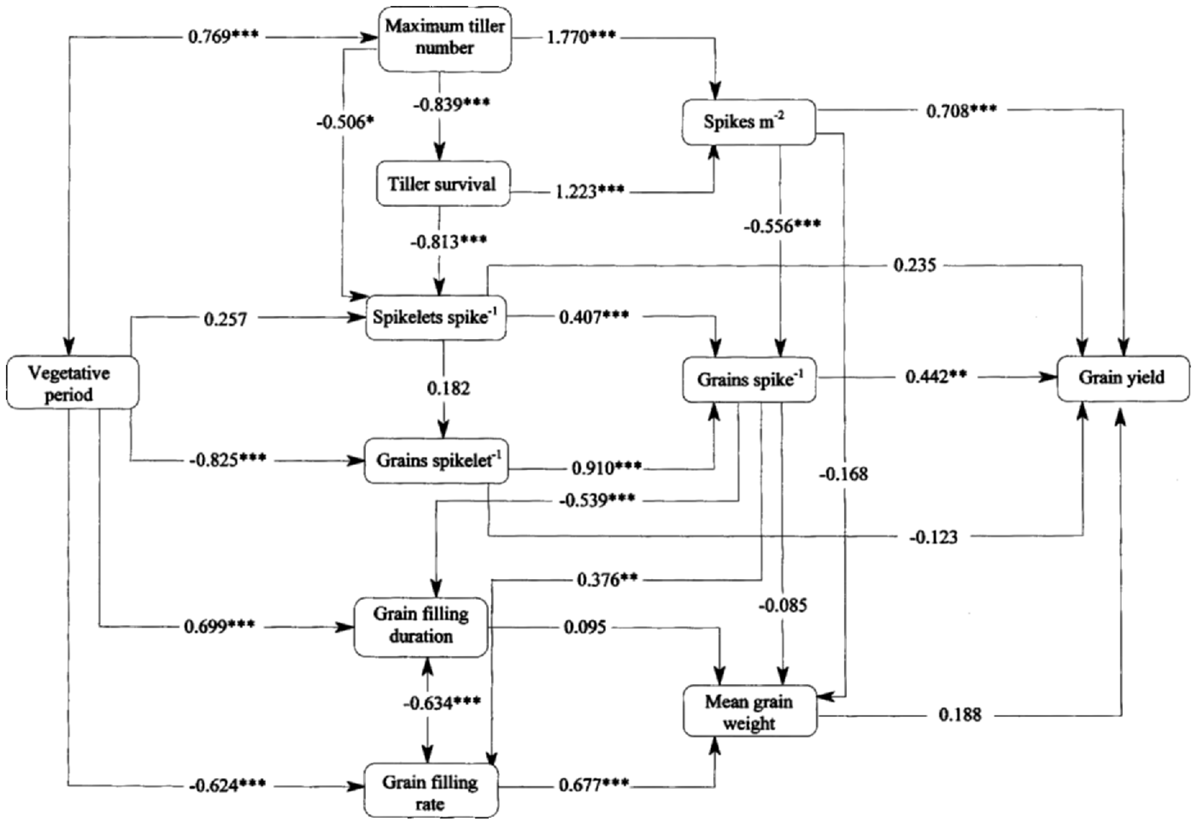

Figure 2. Path-coefficient diagram showing the interrelationships between grain yield, its primary and secondary yield components and the vegetative and grain-filling periods of 25 durum wheat genotypes grown under rainfed conditions during two years (1997 and 1998). The single-headed arrows indicate path coefficients and the double-headed arrows indicate simple correlation coefficients. **,***Significant at 0.01 and 0.001 probability level.

wheat (Slafer & Rawson, 1994) and barley (Willey & Holliday, 1971). Moreover, the experimental decrease of competition for assimilates by removing tillers from the plant in spring wheat resulted in lower floret abortion (Mohamed & Marshall, 1979).

Mean grain weight was influenced equally by the rate and the duration of grain filling under irrigated conditions (Figure 1), whereas in the rainfed site, the grain-filling duration did not significantly affect grain weight, which was determined mainly by the rate of grain growth. The positive relationship between rate and duration of grain filling found in the irrigated site (Figure 1) seems to indicate that when grain maturation is prolonged under conditions with less water deficit, grain growth continues under conditions of high radiation and temperature, which tend to accelerate photosynthesis and translocation of assimilates to the grains. However, under rainfed conditions, a delay in maturity could accentuate water deficit, causing more stomatal closure and consequently reducing photosynthesis and assimilate translocation to the growing grains. This observation seems to be supported in our study by the negative relationship found between rate and duration of grain filling under rainfed conditions (Figure 2). Moreover, this effect could be confirmed by the fact that the duration of vegetative period positively affected the rate of grain filling at the irrigated site and negatively at the rainfed one. While the number of grains spike^{-1} had a positive influence on grain-filling duration under favourable conditions, the relationship became negative in the rainfed environment. This suggests that, under conditions with high water deficit, high sink strength intensifies the competition between growing grains for available resources, thereby limiting grain growth and reducing its duration. However, under both environments, there was a positive relationship between the number of grains spike^{-1} and the rate of grain filling, due probably to a feed-back effect on photosynthesis activity caused by the stimulation of the source capacity as a response to an increase in the sink size (Evans, 1993). Temperature is the main environmental factor affecting rate and duration of grain filling, but large genetic diversity in the response to temperature has been reported in wheat during grain filling (Hunt et al., 1991; Housley & Ohm, 1992).

The duration of the vegetative period (from sowing to anthesis) displayed a positive and significant effect on tiller production at the rainfed site (Figure 2). Therefore, in environments with higher plant competition, enlarging the duration of tillering period could reduce the competition for resources and thus lead to the production and survival of more tillers. At the irrigated site with higher soil fertility, however, tiller production was almost independent of the duration of the vegetative period (Figure 1). In this environment, the number of spikelets spike^{-1} increased as a response to the delay of anthesis; this favoured a large period of floral differentiation that in turn permitted the development and survival of a high number of spikelet primordia (Miralles et al., 2002). However, spikelet fertility was negatively influenced by the anthesis date in both environments, probably because the delay in floret pollination can increase embryo abortion, reducing the number of viable grains per spikelet.

Conclusions

Grain yield decreased significantly under water-shortage conditions mainly as a result of reduction in spikes m^{-2} and grains spike^{-1}. Under these conditions, mean grain weight was less affected and appeared as a relatively stable trait. Under rainfed conditions variations in grain yield were due mainly to spikes m^{-2} followed by grains spike^{-1}, while mean grain weight did not exert a significant influence. However, under favourable conditions, grain yield depended in equal proportion on the three primary yield components.

While compensatory effects were almost absent under irrigated treatments, under water shortage, spikes m^{-2} had a negative effect on grains spike^{-1}, probably due to the inverse relation between tiller production and apical development, arising from the competition for a limited supply of resources during stem and spike growth. The fact that this important negative compensatory effect of the number of spikes m^{-2} on the number of grains spike^{-1} was more evident in the rainfed compared to the irrigated environment may help to explain the restricted success in durum wheat breeding observed in water-limited environments of the Mediterranean region.

Higher yield potential under irrigated conditions was determined by high tiller survival, large fertile spikes and heavier grains. However, under rainfed conditions, characterized by high temperatures and limited tiller formation, the yield components that developed early in the crop cycle (i.e. spikes m^{-2} and grains spike^{-1}) were the most important in determining grain yield.

The percentage of tiller survival was much lower in the irrigated treatment (environment with higher tiller production) than in the rainfed one, supporting the idea that competition for a limited source of assimilates appears to be the main factor affecting tiller abortion in the Mediterranean environments.

Mean grain weight in water-limited environments appears to be conditioned mainly by the rate of grain filling. The existence of genetic variability in wheat for sensitivity to temperature during grain filling could offer the possibility of genetic manipulation of this trait under Mediterranean conditions.

Acknowledgements

This work was financed by Spanish CICYT projects AGF99-0611-C03-01 and AGL2002-04285-C03. Authors wish to thank Dr. Marinetto and A. Cabello for management of field trials. Help of Dr. M. Nachit (ICARDA) on providing useful information about genotypic characteristics is also appreciated. Authors wish to thanks also anonymous reviewers for their valuable comments and criticism and Mr. D. Nesbitt for revising the English version of the text.

References

Bidinger, F.R., R.B. Musgrave & R.A. Fischer, 1977. Contribution of stored pre-anthesis assimilates to grain yield in wheat and barley. Nature 270: 431–433.

Blum, A., 1983. Genetic and physiological relationships in plant breeding for drought resistance. Agr Water Manage 7: 195–205.

Blum, A, B. Sinmena, J. Mayer, G. Golan & L. Shpiler, 1994. Stem reserve mobilisation supports wheat-grain filling under heat stress. Aust J Plant Physiol 21: 771–781.

Davidson, D.J. & P.M. Chevalier, 1990. Preanthesis tiller mortality in spring wheat. Crop Sci 30: 832–836.

Dofing, S.M. & C.W. Knight, 1992. Alternative model for path analysis of small-grain yield. Crop Sci 32: 487–489.

Edmeades, G.O., J. Bolanos, H.R. Lafitte, S. Rajaram, W. Pfeiffer & R.A. Fisher, 1989. Traditional approaches to breeding for drought resistance in cereals. In F.W.G. Baker (Ed.), Drought

Resistance in Cereals, pp. 27–52. ICSU Press: C.A.B. International, Wallingford, UK.
Evans, L.T., 1993. Crop Evolution, Adaptation and Yield. Cambridge University Press: Cambridge.
García del Moral, L.F., J.M. Ramos, M.B. Garcia del Moral & P. Jimenez-Tejada, 1991. Ontogenetic approach to grain production in spring barley based on path-coefficient analysis. Crop Sci 31: 1179–1185.
García del Moral, M.B. & L.F. García del Moral, 1995. Tiller production and survival in relation to grain yield in winter and spring barley. Field Crops Res 44: 85–93.
García del Moral, L.F., D.J. Miralles & G.A. Slafer, 2002. Initiation and appearance of vegetative and reproductive structures throughout barley development. In: G.A. Slafer, J.L. Molina, R. Savin, J.L. Araus & I. Romagosa (Eds.), Barley Science: Recent Advances from Molecular Biology to Agronomy of Yield and Quality, pp. 243–268. Food Products Press, The Harworth Press., New York.
Gibson, L.R. & G.M. Paulsen, 1999. Yield components of wheat grown under high temperature stress during reproductive growth. Crop Sci 39: 1841–1846.
Giunta, F, R. Motzo & M. Deidda, 1993. Effect of drought on yield and yield components of durum wheat and triticale in a Mediterranean environment. Field Crops Res 33: 399–409.
Hamid, Z.A. & J.E. Grafius, 1978. Developmental allometry and its implication to grain yield in barley. Crop Sci 18: 83–86.
Housley, T.L. & H.W. Ohm, 1992. Earliness and duration of grain fill in winter wheat. Can J Plant Sci 72: 35–48.
Hunt, L.A., G. van der Poorten & S. Pararajasingham, 1991. Postanthesis temperature effects on duration and rate of grain filling in some winter and spring wheats. Can J Plant Sci 71: 609–617.
Landes, A. & J.R. Porter, 1989. Comparison of scales used for categorising the development of wheat, barley, rye and oats. Ann Appl Biol 115: 343–360.
Miralles, D.J. & G.A. Slafer, 1999. Wheat development. In E.H. Satorre & G.A. Slafer (Eds.), Wheat. Ecology and physiology of yield determination, pp. 13–43, Food Products Press, The Harworth Press, New York.
Miralles, D.J., R.A. Richards & G.A. Slafer, 2000. Duration of the stem elongation period influences the number of fertile florets in wheat and barley. Aust J Plant Physiol 27: 931–940.
Miralles, D.J., Y. Rharrabti, C. Royo, D. Villegas & L.F. García del Moral, 2002. Grain setting strategies of Mediterranean durum wheat cultivars released in different periods (1900–2000). In: Genotype-Phenotype: Narrowing the Gaps. AAB Conference, Cirencester, UK.
Mohamed, G.E.S. & C. Marshall, 1979. Physiological aspects of tiller removal on spring wheat. J Agric Sci 93: 457–463.
Royo, C., J. Voltas & I. Romagosa, 1999. Remobilization of preanthesis assimilates to the grain for grain only and dual-purpose (forage and grain) triticale. Agron J 91: 12–316.
SAS Institute Inc., 1997. SAS/STAT Software: Changes and Enhancements through Release 6.12. Cary, N.C.
Shpiler, L. & A. Blum, 1991. Heat tolerance to yield and its components in different wheat cultivars. Euphytica 51: 257–263.
Simane, B., P.C. Struik, M.M. Nachit & J.M. Peacock, 1993. Ontogenic analysis of field components and yield stability of durum wheat in water-limited environments. Euphytica 71: 211–219.
Simons, R. G., 1982. Tiller and ear production of winter wheat. Field Crop Abstract 35: 857-870.
Slafer, G.A. & H.M. Rawson, 1994. Sensitivity of wheat phasic development to major environmental factors: A re-examination of some assumptions made by physiologists and modellers. Aust J Plant Physiol 21: 393–426.
Slafer, G.A., D.F. Calderini & D.J. Miralles, 1996. Yield components and compensation in wheat: Opportunities for further increasing yield potential. In: M.P. Reynolds, S. Rajaram & A. McNab (Eds.), Increasing yield potential in wheat: Breaking the Barriers, pp. 101–133. CIMMYT, Mexico.
Willey, R.W. & R. Holliday, 1971. Plant population, shading and thining studies in wheat. J Agric Sci 77: 453–461.
Zadoks, J.C., T.T. Chang & C.F. Konzak, 1974. A decimal code for the growth stages of cereals. Weed Res 14: 415–421.