



Yield formation strategies of durum wheat landraces with distinct pattern of dispersal within the Mediterranean basin

II. Biomass production and allocation

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Abstract

The purpose of this study was to determine if the geographical pattern of dispersal of durum wheat within the Mediterranean region was associated with variation in biomass and leaf area accumulation and distribution, as well as the relationships between these traits and grain yield. Fifty-two landraces previously genetically characterized as dispersed by the north or south of the Mediterranean basin were grown in three rainfed sites in northeastern Spain. The origin of landraces influenced biomass production and allocation. Landraces from the north side of the Mediterranean basin produced 19% more tillers than those from the south, resulting in larger biomass and leaf area allocation on tillers at anthesis. Southern landraces showed a better adaptation to drought environments. They had 6% larger plot stand at jointing, produced 9% more biomass at anthesis and distributed it mostly in the main stem. Besides, they were more efficient in the allocation of biomass to reproductive organs because their mean harvest index (HI) exceeded that of northern landraces by 7%. Crop dry weight (CDW) and leaf area index (LAI) at jointing were positively related to yield in both groups of landraces, whereas at anthesis, no relationship was found between those traits and grain yield. Pre-anthesis assimilates contributed to grain yield by 40 and 90% in northern and southern genotypes, respectively. These results highlight the relevance of early crop development and the remobilization of stored assimilates to grain as adaptive traits to dry Mediterranean environments.

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Keywords: Crop dry weight; LAI; Harvest index; Tillering; Biomass components

Abbreviations: CDW, crop dry weight; LAI, leaf area index; HI, harvest index; DW, dry weight; LAP, leaf area per plant

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1. Introduction

Durum wheat (*Triticum turgidum* L. var *durum*) is mostly grown under rainfed conditions in the Mediterranean region, where drought and heat stress

usually constrain yield potential during the grain filling period (Simane et al., 1993).

Two routes of dispersal have been hypothesized for durum wheat within the Mediterranean basin, one through southern Europe, occurred from 10,000 B.P. (before present) to 7000 B.P. (Feldman, 2001), and a second one, much more recent, through North Africa (Moragues et al., submitted). Contrasting grain yield formation strategies between genotypes adapted to the two regions are reported in the first paper of this series (Moragues et al., 2006). Thus, landraces dispersed through the north of the Mediterranean basin, which has a colder and wetter climate than the south (Leemans and Cramer, 1991), based their yield on weight per grain, while the number of spikes per m² was the most important yield component explaining yield variation of the genotypes dispersed through the south. On the basis of these results, we hypothesized that the zone of adaptation may also have affected biomass accumulation and allocation, as well as leaf area, and their relationships with grain yield.

Grain yield can be expressed as the result of three physiological processes: radiation interception by photosynthetic organs, conversion of the intercepted radiation into dry matter and partitioning of that dry matter, as expressed by harvest index (HI) (Hay and Walker, 1989). The first process is related to the photosynthetic area and, therefore, to leaf area index (LAI); the second one is related to photosynthetic efficiency. Total biomass or crop dry weight (CDW) is the result of these two processes. Harvest index (HI) is the ratio of grain yield to biological yield, i.e., a measure of the efficiency of the plant when accumulating assimilates in the organs of economic significance (Donald, 1962, 1968).

Significant relationships between yield and biomass at anthesis or during grain filling have been reported in bread wheat (Turner, 1997), barley (Ramos et al., 1985) and durum wheat (Boggini et al., 1990; Villegas et al., 2001; Ramdani, 2004). In small grain cereals biomass or leaf area in early developmental stages has also been positively related to grain yield under Mediterranean-type environments, due to the reduction of soil water losses from evaporation and the increase in water use efficiency (the relationship between yield and water available to the crop through precipitation and/or irrigation),

when growth occurs in the cool period of the season (López-Castañeda and Richards, 1994a; Hafid et al., 1998).

Water stress may affect the growth of wheat, but the effects are small when stress occurs in the early stages than when it occurs in the late vegetative phase and during grain filling (Abayomi and Wright, 1999). Both dry weight per plant and total above-ground biomass are affected by drought as consequence of a decrease in the rate of growth (Villegas et al., 2001). Genotypes most efficient in the use of water are characterized, among others, for the following traits: (i) increased transfer of the water available through the crop limiting evaporation from the soil surface or drainage beyond the root zone; (ii) large transpiration efficiency; and/or (iii) efficiency in partitioning more of the achieved biomass into grain (Condon et al., 2004). Evaporative losses from the soil surface may be reduced by a good stand establishment and early seedling vigour, since the rapid development of leaf area results in more light interception, contributing to shade the soil surface from direct solar radiation (Condon et al., 2004). In addition, reducing water evaporation from the soil surface maximizes crop transpiration and improves the ratio transpiration/evapotranspiration (Condon and Richards, 1993; Richards et al., 2002).

The process of tillering has been found to be relevant for yield formation in small grain cereals (García del Moral et al., 1991; Dofing and Knight, 1992). Under field conditions, the number of tillers increases rapidly until a maximum reached shortly after floral initiation, then diminishes rapidly before spike emergence, and then stabilizes until harvest (García del Moral et al., 1984; Royo and Tribó, 1997). Tiller mortality often begins after floral initiation of the main shoot, as developing tillers compete for resources with developing spikelets and florets on the main stem (Miralles and Slafer, 1999). Tillers that emerge late during plant development seem to be most likely to senesce prematurely (Davidson and Chevalier, 1990).

The aim of this work was to assess if the geographical pattern of distribution of durum wheat within the Mediterranean basin affected biomass accumulation, leaf area expansion and their distribution within the plant, as well as the relationships between these traits and grain yield.

2. Materials and methods

2.1. Plant material and experimental design

Three field experiments were carried out during 2001–2002 crop season under rainfed conditions in three sites of northern Spain (Gimenells, Castelló de Farfanya and Foradada). These testing environments are located in a temperate-dry area with intermediate climate characteristics between the extreme cold and dry environments typical of the north-east and the south-east of the Mediterranean basin, respectively. The three sites differ in their soils, weather conditions and agronomic practices done by farmers, thus leading to a range of yield potentialities (see Moragues et al., 2006). Average temperatures during growth cycle were 10.9, 11.2 and 9.8 °C, and cumulative rainfall was 186, 281 and 371 at Gimenells, Castelló de Farfanya and Foradada, respectively. December was the coldest month with average temperatures close to 0 °C in the three sites. Precipitation during winter (December–March) was of 54.6, 52.8 and 84.6 mm at Gimenells, Castelló de Farfanya and Foradada, respectively, while temperatures increased very fast during this period in the three sites (see Moragues et al., 2006 for details).

Fifty-two durum wheat landraces were classified in a previous study by means of molecular markers as having been dispersed from the center of origin through the north or the south of the Mediterranean basin (Moragues et al., submitted). These were used in this investigation. Sixteen of them, coming from Turkey, Cyprus, Greece, Italy and Portugal, corresponded to the northern dispersal group, and the remaining thirty-six, coming from Syria, Lebanon, Egypt, Greece, Algeria, Italy, Morocco, Spain and Portugal, corresponded to the southern dispersal. Details on the genotypes may be found in Moragues et al. (2006).

Plot layout and experimental design have been previously described (Moragues et al., 2006). In brief, the design consisted of alpha-lattice incomplete-block designs with three replicates and three locations. The seeding rate was adjusted to 250 viable seeds m⁻². Plot size was 4.8 m² (8 rows, 0.15 cm apart and 4 m length). Each plot was divided in two parts, each 2 m in length; one used for destructive sampling and the other for yield evaluation.

2.2. Biomass measurements

For biomass determinations, the plants contained in 0.5 m row length were uprooted at random from a central row of each plot at the first node-detectable stage (E.31 of the Zadoks' scale (Zadoks et al., 1974)) and at mid-anthesis (E.65 of the same scale). Border lines were excluded for sampling. At each sampling occasion not less than 15 cm were left from a previous sampled area in the same row, and care was taken that adjacent rows had intact plant populations. The number of plants and tillers were counted in the whole sample at jointing, whereas at anthesis, the number of tillers, leaves and spikes were determined on a random sub-sample of five plants per plot. Senesced and dead leaves were not taken into account. Leaf sheaths were not removed from the stems, so in this paper, stem weight includes sheath weight in all cases. At both sampling stages, the components of plant biomass and leaf area were determined separately for the main stem and tillers.

Leaf area (one side) was measured using a leaf area-meter (AT Delta-T-Dias II), excluding from the measurement yellow and dry leaves. Samples were oven dried at 70 °C for 48 h, and weighed. Crop dry weight and leaf area index were calculated as follows: CDW (g m⁻²) = $N \times W$, where N is the number of plants m⁻² and W is the weight per plant (g per plant); LAI = $N \times LAP$, where LAP was the leaf area per plant (cm²). Plant height (cm) was measured from the soil to the top of the spike without considering awns length.

The number of days from sowing to jointing, and from sowing to anthesis were determined for each plot, and the relative growth rate (RGR) for CDW and LAI were calculated as follows (Kvet et al., 1971):

$$\text{RGR} = \frac{\ln V_j - \ln V_a}{t_a - t_j}$$

where V_j and V_a are the values of the traits measured at jointing and anthesis, and t_j and t_a are the number of days from sowing to jointing and anthesis, respectively. RGR was multiplied by 7 to express it on a weekly basis. At ripening, 1 m length of a central row was uprooted and the weight of shoots (stems and leaves), spikes and grains were determined. Harvest index was calculated as the ratio between grain and plant weight on the whole sample.

Remobilization of pre-anthesis assimilates was assessed according to two alternative parameters (Papakosta and Gagianas, 1991), DM translocation (DMT, g/m²) and the contribution of pre-anthesis assimilates to the grain (CPAAG, %):

$$\text{DMT} = \text{DM}_{\text{anthesis}} - (\text{DM}_{\text{maturity}} - \text{grain yield})$$

$$\text{CPAAG} = \left(\frac{\text{DMT}}{\text{grain yield}} \right) \times 100$$

2.3. Statistical analyses

Combined analyses of variance were performed for all the growth traits measured (see Moragues et al., 2006 for description). The Tukey's test (Hsu, 1996) was used to determine the significance of the differences between dispersal groups. Stepwise regression analyses were carried out to assess the contribution of biomass traits to grain yield. SAS (SAS Institute Inc., 2000) procedures and programs were used for these calculations.

3. Results

3.1. Biomass accumulation and leaf area expansion

The ANOVA revealed that the site exerted a significant effect on all traits analyzed excepting LAI at anthesis and DMT (Table 1). Differences between dispersal groups were significant for CDW at anthesis, HI, plant height and DMT, but both groups had similar LAI values both at jointing and anthesis and growth rates for CDW and LAI. A significant non-crossover site \times dispersal group interaction for HI occurred. The partition of the genotype effect into its components showed that differences between genotypes for CDW and LAI were mostly due to the variability existing within the southern landraces. However, for HI, plant height and growth rate of LAI, variability existed within both dispersal groups. Statistically significant differences for growth rate of CDW appeared only within northern landraces (Table 1). Southern landraces showed 9% higher CDW at anthesis, 7% higher HI, 3% taller plants and 121% more dry matter translocation than northern ones (Table 2). The contribution of pre-anthesis accumulated reserves to grain filling averaged 40.1

and 89.7% in northern and southern landraces, respectively.

3.2. Biomass and leaf area distribution

In order to ascertain whether differences between the two dispersal groups existed in the distribution of biomass and leaf area, CDW and LAI were partitioned into their components and sub-components at jointing and anthesis. At jointing, southern landraces had 6% more plants per m² and higher dry weight and leaf area on the main stem than northern ones (upper part of Table 3). This was a general pattern, though differences on main stem weight (8%) and dry weight of leaves on main stem (4%) were non-significant. In contrast, northern landraces had 19% more tillers per plant, which weighed 17% more and had 7% more leaf area than those of southern genotypes, thus accounting for the significantly higher weight per plant of stems and leaves of tillers in northern landraces (Table 3). The number of plants per unit area was similar at anthesis and jointing, indicating that plant mortality did not occur between these stages.

In order to explore if the effect of the different plant density on northern and southern genotypes biased the results of the ANOVA, analyses of covariance were carried out for all the studied traits using the number of plants per m² as a covariate. Although the number of plants per m² was significant for the components of biomass and leaf area at both jointing and anthesis, the differences between groups were consistent with the results obtained from the ANOVA (Table 3).

At anthesis, southern landraces had 16% more weight on the main stem than northern ones and this was reflected in weights of all of its components (lower part of Table 3). Leaf area on the main stem was 16% greater in southern genotypes because their leaves were 19% larger and 20% heavier. However, at anthesis they had fewer green leaves on the main stem and on tillers than northern landraces.

Conversely, northern landraces tended to have greater tiller weight per plant due to greater weights of all their components, but these differences were not statistically significant (Table 3). However, the weight of each individual tiller was significantly higher in southern landraces, due to heavier stems, leaves and

Table 1

F values of the analyses of variance for crop dry weight (CDW) and leaf area index (LAI) at jointing and anthesis, relative growth rates of CDW and LAI, dry matter translocation (DMT), harvest index (HI) and plant height of 52 Mediterranean durum wheat landraces divided in two groups according to their pattern of dispersal

Source of variation	d.f.	CDW			LAI		Relative growth rate		DMT	HI	Plant height
		Jointing	Anthesis	Maturity	Jointing	Anthesis	CDW	LAI			
Site	2	149 ^{***}	11.2 ^{**}	28.4 ^{***}	103 ^{***}	1.00	161 ^{***}	27.5 ^{***}	1.10	169 ^{***}	20.6 ^{**}
Dispersal	1	0.01	7.40 ^{**}	0.77	0.07	1.30	1.96	0.61	9.16 ^{**}	4.93 [*]	23.2 ^{***}
Site × dispersal	2	0.68	1.14	1.48	1.84	1.25	1.53	1.91	0.12	5.71 ^{**}	0.55
Genotype (dispersal)	50	2.06 ^{***}	1.14	1.60 [*]	3.23 ^{***}	1.91 ^{***}	1.98 ^{***}	2.40 ^{***}	1.18	2.71 ^{***}	7.50 ^{***}
Within north	15	1.26	0.72	2.03 [*]	1.23	0.93	3.23 ^{***}	2.04 [*]	1.01	3.16 ^{***}	5.82 ^{***}
Within south	35	2.41 ^{***}	1.29	1.45	4.10 ^{***}	2.33 ^{***}	1.47	2.58 ^{***}	1.25	2.45 ^{***}	8.12 ^{***}
Site × genotype (dispersal)	100	1.39 [*]	0.98	1.00	1.49 ^{**}	1.30	1.28	1.45 [*]	1.07	1.52 ^{**}	1.26
Site × within north	30	1.00	0.96	0.68	0.98	0.91	1.93	0.85	0.83	1.19	1.34
Site × within south	70	1.57 ^{**}	0.99	1.15	1.73 ^{**}	1.50	1.01	1.70 ^{**}	1.17	1.70 ^{**}	1.23
Rep (site)	6	0.000	250	0.000	0.002	0.012	0.000	2.1×10^{-6}	602	0.000	2.838
IB (rep × site)	99	80.55	5611	12028	0.014	0.054	1.8×10^{-8}	1.8×10^{-5}	0.000	0.001	15.01
Residual	206	1533	44998	33599	0.102	0.206	6.5×10^{-7}	1.3×10^{-4}	79859	0.003	86.98
Total	466										

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 2

Adjusted means and standard deviation of crop dry weight (CDW) and leaf area index (LAI), relative growth rates of CDW and LAI, dry matter translocation, harvest index (HI) and plant height for the two dispersal groups

		North (a)	South (b)	Difference between groups (a – b)/a × 100 (%)
CDW (g/m ²)	Jointing	132 ± 15.2	132 ± 21.1	0
	Anthesis	679 ± 62.8	741 ± 86.5	–9**
	Maturity	859 ± 19.8	841 ± 15.2	2
LAI	Jointing	1.30 ± 0.12	1.29 ± 0.23	1
	Anthesis	1.40 ± 0.16	1.46 ± 0.26	–4
Relative growth rates from jointing to anthesis	CDW (week ^{–1})	0.371 ± 0.063	0.386 ± 0.041	–4
	LAI (week ^{–1})	0.022 ± 0.038	0.030 ± 0.049	–36
Dry matter translocation (g/m ²)		97 ± 26.0	214 ± 18.8	–121**
HI		0.28 ± 0.04	0.30 ± 0.03	–7*
Plant height (cm)		122 ± 7.92	126 ± 9.34	–3***

* $P < 0.05$ according to Tukey's test.

** $P < 0.01$ according to Tukey's test.

*** $P < 0.001$ according to Tukey's test.

Table 3

Adjusted means and standard deviation of the number of plants per m² and biomass traits per plant, determined at jointing and anthesis for the two dispersal groups

		North (a)	South (b)	Difference between groups (a – b)/a × 100 (%)
Jointing				
Number of plants per m ²		110 ± 15.0	117 ± 17.8	–6*
Number of tillers per plant		2.71 ± 0.65	2.20 ± 0.57	19***
Dry weight (g)	Plant	1.30 ± 0.26	1.26 ± 0.25	4
	Main stem	0.59 ± 0.08	0.64 ± 0.11	–8
	Tillers	0.75 ± 0.21	0.62 ± 0.18	17***
Stem dry weight (g)	Main stem	0.33 ± 0.05	0.36 ± 0.07	–9*
	Tillers	0.37 ± 0.11	0.32 ± 0.09	14*
Leaves dry weight (g)	Main stem	0.26 ± 0.03	0.27 ± 0.05	–4
	Tillers	0.38 ± 0.10	0.30 ± 0.09	21***
Leaf area (cm ²)	Main stem	51.8 ± 5.8	56.3 ± 8.3	–9**
	Tillers	131 ± 23.0	122 ± 25.3	7**
Specific leaf area (cm ² /g)	Plant	210 ± 9	217 ± 12	–3**
	Main stem	201 ± 8	210 ± 12	–4***
	Tillers	218 ± 12	226 ± 13	–4*
Anthesis				
Number of plants per m ²		111 ± 11.2	117 ± 15.7	5
Number of tillers per plant		2.07 ± 0.45	1.63 ± 0.34	21***
Number of leaves	Plant	9.6 ± 1.35	8.32 ± 1.04	13**
	Main stem	3.69 ± 0.25	3.57 ± 0.21	3**
	Tillers	5.91 ± 1.31	4.75 ± 1.08	20***
Number of spikes per plant		2.34 ± 0.41	2.05 ± 0.35	12***
Dry weight (g)	Plant	6.5 ± 0.36	6.71 ± 0.57	–3
	Main stem	3.12 ± 0.75	3.63 ± 0.61	–16***

Table 3 (Continued)

		North (a)	South (b)	Difference between groups (a – b)/a × 100 (%)
	Tillers	3.38 ± 0.75	3.08 ± 0.88	9
Stem dry weight (g)	Main stem	2.13 ± 0.54	2.50 ± 0.66	-17***
	Tillers	2.32 ± 0.50	2.12 ± 0.43	9
Leaves dry weight (g)	Main stem	0.38 ± 0.04	0.44 ± 0.08	-16***
	Tillers	0.49 ± 0.12	0.44 ± 0.11	10
Spike dry weight (g)	Main stem	0.60 ± 0.08	0.70 ± 0.11	-17***
	Tillers	0.56 ± 0.15	0.51 ± 0.12	9
Dry weight (g/tiller)	Stem	1.15 ± 0.18	1.35 ± 0.23	-17***
	Leaves	0.24 ± 0.03	0.27 ± 0.06	-13**
	Spikes	0.27 ± 0.05	0.31 ± 0.06	-15***
Mean weight of one leaf (g)	Main stem	0.10 ± 0.01	0.12 ± 0.02	-20***
	Tillers	0.08 ± 0.01	0.09 ± 0.01	-12**
Leaf area (cm ²)	Main stem	55.5 ± 8.78	64.6 ± 15.4	-16***
	Tillers	78.5 ± 16.8	68.8 ± 18.6	12*
Mean area of one leaf (cm ²)	Main stem	15.1 ± 2.04	18.0 ± 3.87	-19***
	Tillers	13.3 ± 2.10	14.3 ± 3.12	-7
Specific leaf area (cm ² /g)	Plant	162 ± 13	158 ± 17	2
	Main stem	152 ± 15	151 ± 16	~0
	Tillers	178 ± 22	173 ± 32	~0

* $P < 0.05$ according to Tukey's test.

** $P < 0.01$ according to Tukey's test.

*** $P < 0.001$ according to Tukey's test.

spikes (17, 13 and 15%, respectively). Therefore, the higher weight of tillers per plant of northern landraces was only due to the larger number of tillers. This association of higher tiller number with smaller size was also observed at a leaf level. Thus, northern landraces had 3% ($P < 0.01$) and 20% ($P < 0.001$) greater number of leaves on main stem and tillers, but they weighed 20% ($P < 0.001$) and 12% ($P < 0.01$) less, respectively. The mean leaf areas on both main stem and tillers were 19% ($P < 0.001$), and 7% (ns) lower in northern than in southern genotypes, respectively. These compensatory effects between weight and number may be due to competition for available resources.

3.3. Changes in tiller number

The average number of tillers per m² was determined for each dispersal group at three different developmental stages: jointing, anthesis and ripening, and the pattern of changes is shown in Fig. 1. Northern

landraces had a significantly higher number of tillers at jointing (Table 3; Fig. 1), anthesis (Table 3; Fig. 1) and ripening (Fig. 1). Large tiller mortality was observed between jointing and anthesis in both groups

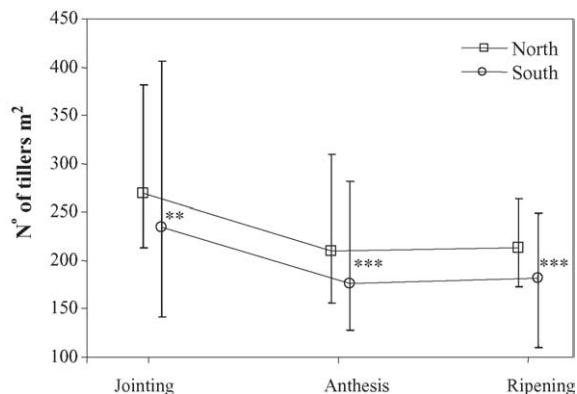


Fig. 1. Changes on tiller number for each dispersal group. Vertical bars indicate range of adjusted mean values. ** $P < 0.01$, *** $P < 0.001$.

of germplasm, but after anthesis the number of tillers per m² remained stable.

3.4. Relationships between yield and biomass and LAI

Step-wise regression analyses were performed to identify the biomass traits that better explained variations in grain yield for each group of genotypes. Crop dry weight and LAI at jointing and anthesis were included as dependent variables in the analysis. The only variable that entered the model for the northern group was CDW at jointing and it explained 72% of yield variations (Fig. 2a). For the southern group, the

only variable entered was LAI at jointing with an R^2 of 0.56 (Fig. 2d).

4. Discussion

4.1. Biomass and leaf area production and allocation

The two groups of genotypes produced the same average amount of biomass during early growth stages. The fact that southern landraces had 6% more plants per m² but about 6% less biomass per plant led to the production of similar above-ground biomass.

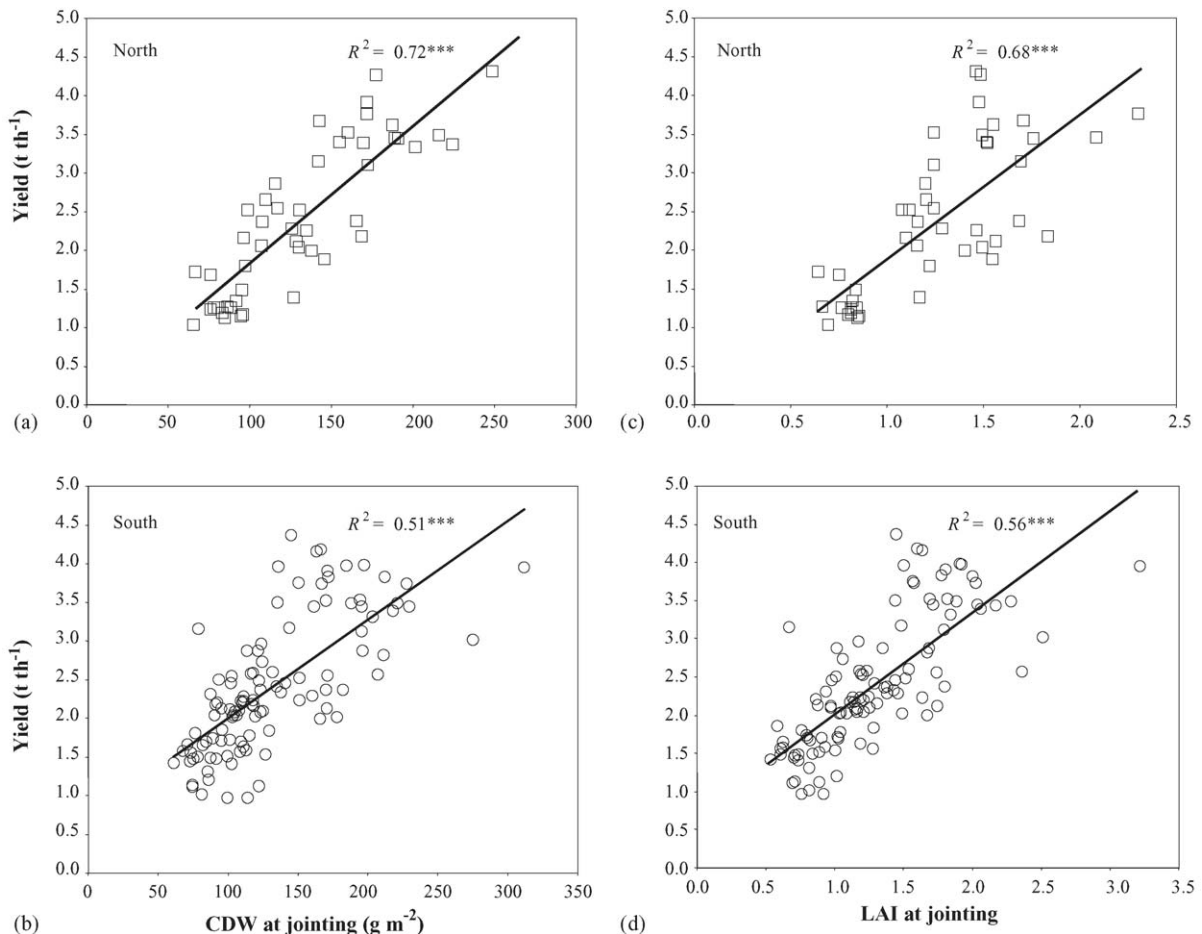


Fig. 2. Relationships between yield and crop dry weight (CDW) (a and b), and between yield and leaf area index (LAI) (c and d) at jointing for both dispersal groups. Each point represents genotype means for each of three rainfed environments.

Since the same sowing density was used for all genotypes, these results suggest higher plant mortality during early growth stages for northern landraces, probably because southern genotypes were able to survive better under the dry conditions prevalent during winter. Different authors have reported a negative effect of drought on seedling survival and growth (Blum, 1996; Mian and Nafziger, 1994). The larger plot stand detected on southern genotypes from jointing onwards should have resulted in more biomass production at early stages. However, both northern and southern genotypes had similar biomass at jointing, suggesting superior genetic potential for early growth in northern than in southern landraces.

Moreover, biomass distribution within the plant differed between groups. The higher weight per plant in the northern landraces was due to their superior tillering capacity, since they had 19% more tillers per plant than southern ones (Table 3). The lower plant density of northern genotypes probably contributed to the large tillering capacity and the size of tillers as tiller production increases as plant densities decrease (Rahnama et al., 1995). However, only about 6% of increase in tiller production would have been expected due to 6% lower plant density, if compensation had been perfect, but the observed 19% difference was indeed a consequence of a greater tillering capacity of northern landraces. Northern Mediterranean durum wheat landraces were very efficient in the production of tillers, but equally inefficient at maintaining them since one-fourth of tillers produced died before anthesis. This was probably the cause of the huge reduction in the leaf area on tillers (40 and 44% in northern and southern genotypes, respectively), from jointing to anthesis. Competition among shoots for nutrients, light and water seems to be the principal cause of tiller mortality (García del Moral and García del Moral, 1995).

The differences in growth rates between jointing and anthesis were not significant, though southern landraces tended to have higher mean growth rates resulting in a significant 9% greater biomass (mostly due to that allocated on main stems) at anthesis of southern landraces compared to northern ones. This result may be consequence of a better adaptation of the southern dispersal group to warm and dry environments, given that from jointing to anthesis temperatures rose very fast and the soil was depleted because of the scarcity of rain.

Differences between groups in biomass at anthesis were probably associated with the heavier main stems and their three components (stem, leaves and spikes), and a greater leaf area on main stem in the southern group of genotypes. It could be a consequence of a faster growth of roots of southern genotypes that would enable them to exploit deeper soil layers improving their water use (Richards et al., 2002).

The unimproved landraces evaluated herein showed much lower values of biomass and LAI at jointing and anthesis compared to other studies that used modern varieties and higher plant densities under irrigated environments (Giunta et al., 1995; Villegas et al., 2001; Royo et al., 2004). On the other hand, when comparing with the results found by Hafid et al. (1998) under water-stressed conditions, the landraces in this study had higher LAI at jointing, but less at anthesis, probably because in the study of Hafid et al. (1998), irrigation was provided before anthesis. From jointing to anthesis LAI increased 8 and 13% in northern and southern landraces, respectively. The larger increase of the LAI in southern genotypes was a consequence of their higher growth rate of leaf area likely consequence of their better tolerance to heat and drought stresses.

Crop dry weight at anthesis was 9% higher in the southern genotypes because the two components (number of plants per m² and weight per plant) reached higher values, even though they did not differ significantly between groups. However, the largest differences between groups arose from their different strategies for allocating biomass within the plant. In northern genotypes, biomass was more concentrated in tillers than in the main stem, and the opposite was true for southern genotypes. In northern landraces, 44 and 48% of the total dry weight of the plant was on the main stem at jointing and anthesis versus 51 and 54% at jointing and anthesis, respectively in the southern group. These tendencies were driven by differences in the largest component, stem dry weight. The distribution of leaf area at both jointing and anthesis and spike weight at anthesis followed the same trend. Southern lines, being better adapted than northern to drier environments, have relied more on the productivity of the main stem, while northern genotypes have emphasized the role of tillers. This assumption is supported by the larger number of stems per m² found at ripening in northern genotypes compared to southern ones. Our results show that northern land-

ances, which have evolved in colder environments than southern landraces, showed a higher number of smaller tillers with a higher number of smaller leaves on the main stem and lower growth rates when evaluated in drought stress environments. Varieties developed under cooler conditions increased their tillering capability because tiller production is favored by low temperatures, probably at expense of growth of leaves, tillers and inflorescences (Kirby and Riggs, 1978; García del Moral and García del Moral, 1995).

Harvest index of Mediterranean landraces, as expected, was lower than the reported for modern semi-dwarf cultivars, but similar to those found by Merah and Monneveux (2001) in a durum core collection that included a large number of landraces. Remobilization of pre-anthesis assimilates to grain was more than double, and harvest index was 7% greater in the southern group of dispersal than in the northern, probably because in southern landraces, dry matter was partitioned to more soluble carbohydrates that were later mobilized to the grain (Richards et al., 2002). This suggests a higher capacity to allocate biomass into grains and likely also a better ability to set grains under stress. The greater harvest index of southern genotypes may also indicate that they were more efficient in using water in post-anthesis than northern landraces (Condon et al., 2004), which is a sign of adaptation to drought environments. In addition, the huge contribution of stored assimilates to grain filling in southern landraces points out that pre-anthesis storage carbohydrates were critical for yield formation on this group. This also suggests a better adaptation of southern landraces to drought environments in which terminal stresses limit transient photosynthesis, and grain growth has to be mostly supported by translocation of stored reserves (Shepherd et al., 1987; Papakosta and Gagianas, 1991).

4.2. Relationships between yield biomass and leaf area accumulation and distribution

In both groups of germplasm, biomass and LAI at jointing were more related to yield than the same traits measured at anthesis. Nevertheless, many studies carried out with modern varieties have reported significant relationships between yield and biomass at anthesis (Ramos et al., 1985; Turner, 1997; Villegas et al., 2001). However, in this study, neither biomass

nor LAI at anthesis were significantly correlated with yield. It could be due to the lack of dwarfing genes in the landraces, while modern varieties have higher HI and reduced plant height as consequence of the introduction of dwarfing genes (Bozzini, 1970; Vallega and Zitelli, 1975).

The results of this investigation suggest that early development was essential for grain production probably because high biomass production and leaf area development at early developmental stages contributed to a rapid cover of the ground surface, favoring root development, increasing carbon capture and reducing soil water evaporation, as has been reported in durum wheat (Acevedo et al., 1991; López-Castañeda et al., 1996; Hafid et al., 1998) and other small grain species (Richards and Townley-Smith, 1987; Turner and Nicolas, 1987). Early vigour is an important adaptation trait of durum wheat to terminal drought in Mediterranean environments (Van Oosterom and Acevedo, 1992; López-Castañeda and Richards, 1994b; Villegas et al., 2000).

5. Concluding remarks

The results of this research show that the environmental conditions of the areas of spread of durum wheat across the Mediterranean basin determined the strategy of the crop to produce and allocate biomass. Landraces that spread along the north side of the Mediterranean Sea, with more favorable climatic conditions, emphasized tiller production and concentrated most of the biomass and leaf area at anthesis in more tillers. This strategy would allow the plant to develop a high yield potential in favorable environments. This contrasts with landraces evolved in the south of the Mediterranean basin, where prevalent weather conditions are hotter and drier. These were more efficient in the production of biomass at anthesis when cultivated under rainfed conditions, showing a better adaptation to drought environments probably associated to a greater water use efficiency during grain filling. Moreover, their strategy of concentrating a larger amount of biomass on the main stem rather than in tillers was more efficient in terms of biomass allocation to productive organs.

The fact that the best relationship between biomass and yield was found at jointing underlines the

importance of early development for grain yield. Besides, the large contribution of pre-anthesis assimilates to grain yield on southern landraces highlights the role of remobilization of stored reserves on grain yield in genotypes adapted to dry Mediterranean environments.

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