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Seedling development and biomass as affected by seed size and morphology in durum wheat

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SUMMARY

This work evaluated the effect of seed size and morphology on the development and biomass of durum wheat seedlings. Three different seed-grading sizes selected by sieving were used in glasshouse experiments, and a set of three developmental and 23 biomass-related indices were measured on eight genotypes, at two moisture levels. The influence of seed size on seedling development was studied at high and low temperatures (22/12 °C, and 15/5 °C day/night temperatures, respectively), in growth chambers.

The area of the seed and the area of the embryo were the seed morphological traits most affected by seed size. Seed size was strongly associated with seedling development and seedling biomass until the complete extension of the first two leaves, at the fourth leaf stage. The rate of first-leaf growth and the area of the first leaf were the developmental and biomass traits, respectively, most sensitive to seed-grading size.

INTRODUCTION

Durum wheat is an important winter cereal crop in the Mediterranean region, where drought stress is the main environmental constraint to grain yield. Rapid seedling establishment and early growth have been suggested as useful traits for improving yield under Mediterranean conditions (Acevedo *et al.* 1991; López-Castañeda *et al.* 1996). Thus, Turner & Nicolas (1987) showed a positive relationship between early vigour and grain yield for 22 bread-wheat genotypes. Moreover, genetic variability for early vigour has been demonstrated in temperate cereals other than durum wheat (Turner & Nicolas 1987; Richards 1987, 1996; Regan *et al.* 1992). The positive influence of early vigour on yield potential has been attributed to reduced evaporation from the soil surface due to greater ground cover (Fischer 1981; Richards 1987) and to increased radiation interception (Ludlow & Muchow 1990).

It is generally accepted that seed size may influence seedling emergence (Lafond & Baker 1986; Mian & Nafziger 1994) and development (Bremner *et al.* 1963; Evans & Bhatt 1977), and hence early vigour within a species (Evans & Bhatt 1977; Halloran & Pennell 1982; Lafond & Baker 1986; Peterson *et al.* 1989). It has been reported that selecting for seedling vigour could be done in spring bread wheat by looking for greater seed mass, associated with a shorter emergence time and a faster rate of plant development (Lafond & Baker 1986).

Most of the studies on the relationship between seed characteristics and early vigour have been performed by comparing different cereal species (such as barley and bread wheat) with a contrasting constitutive expression for these traits (Pinthus & Osher 1966; Halloran & Pennell 1982; López-Castañeda *et al.* 1996). Thus, irrespective of their seed size, the greater early vigour of barley compared with bread and durum wheat, oat and triticale has been associated with its larger embryo, which results in more expanding cells after imbibition and more vigorous early root and shoot growth (López-Castañeda *et al.* 1996; Richards 1996). However, this scenario is far less clear when the relationship is studied within a given species. Some authors conclude that the amount of endosperm and aleurone tissue is

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more important than the embryo in determining early vigour in bread wheat, since seed reserves are essential during germination and further seedling emergence (Bremner *et al.* 1963; Lowe & Ries 1973; Peterson *et al.* 1989). This information, however, is lacking for durum wheat. On the other hand, developmental and growth traits (such as fast leaf-area development, high dry-matter production and high leaf-area), are usually considered together when the effect of seed size on early vigour is studied, since both traits are important contributors to early vigour. Studies concerning the relationship between seed size and developmental rates and seedling growth, considered independently, are scarce.

The aim of this study was to investigate the seed morphological and the seedling developmental and biomass traits most related to seed size. Glasshouse and growth chamber experiments were conducted on durum wheat genotypes from different origins within the Mediterranean region, and which were chosen to cover a wide range of genetic variability.

MATERIALS AND METHODS

Plant material

Eight durum wheat (*Triticum turgidum* L. var. *durum*) genotypes were used for the glasshouse experiments: four Spanish commercial varieties (Altar-Aos, Mexa, Vitrón and Jabato), and four genotypes from the Eastern Mediterranean region bred in the CIMMYT/ICARDA durum programme: two commercial varieties (Korifla and Omrabi-3) and two advanced lines (Sebah and Awaltbit). Altar-Aos, Vitrón, Jabato and Sebah were used in the growth chamber experiment. All seeds were obtained from field-grown plants harvested the previous year.

Seed morphology

Seeds of each genotype were divided into three sizes according to the round-hole-diameters of the sieves used to separate them. The grading size (i.e. the diameter of the seed) of the three sets of seeds were 3·4–3·5 mm for large seeds, 2·2–2·5 mm for medium seeds, and 1·8–2 mm for small seeds. In this paper, the seed diameter is referred to as seed size. For morphological determinations, five seeds were taken at random from each genotype and grading-size, and fixed in a mixture (w/w) of 5% pure acetic acid, 5% neutral formic aldehyde (40%, w/w) and 90% ethanol (70%, w/w). The seeds were cut with a freezing microtome on a plane approximately at right angles to the ventral furrow (dorsiventral) plane. The seed sections were stained with Lugol (5% I_2 and 10% KI w/w in distilled water) and digitized with a binocular microscope (Leica-MZ8) equipped with a video camera. For each seed section, the length of the major axis of the seed, the perimeter and the sectional area of the seed and the embryo, and the width and length of the embryo were determined with the aid of the Leica Qwin image-analysis programme.

Glasshouse experiments

Two sets of glasshouse experiments were performed simultaneously, each one under a different water regime. One was daily irrigation, to maintain the soil at field capacity or close to it, and the other consisted of irrigating every third day to simulate growth under limited water conditions.

Each experiment comprised a randomized complete-block design with four replicate blocks, and with the 24 combinations of the eight genotypes and three seed sizes randomized within each block. The seeds were placed in trays of 15 square cells, each of 7·5 cm width and 8 cm height. The cells were filled with a sterilized, fertile, compost-based potting mix. Each experimental plot consisted of four cells containing a total number of 12 seeds (three seeds per cell), sown at a depth of 3 cm; thus, each tray contained three plots of four cells and three unsown cells. Both experiments were conducted under a natural seasonal photoperiod (11–12 h daylight) and within a maximum day/night temperature of 25/15 °C.

Thermal time was calculated in growing degree-day units (GDD, °C) by adding the daily values of mean temperature above a base temperature of 0 °C (Gallagher 1979). The date of emergence was recorded when 90% of the seedlings had emerged (Regan *et al.* 1992). The Haun stage (Haun 1973) was determined twice a week for each treatment. The rate of development was measured by the following indices: thermal duration to plant emergence (GDD from planting to the appearance of the first leaf), rate of first-leaf growth (mg/GDD, measured as the weight of the first leaf fully expanded/GDD from planting to the complete expansion of this leaf), and rate of appearance of the first four leaves (number of leaves/GDD).

Biomass measurements were made when the least developed seedlings of each treatment reached four leaves (growth stage 14; Zadoks *et al.* 1974). At this time, the most advanced seedlings within each treatment had five extended leaves. Number of leaves, stem length and area, and the length, width and area of each leaf in the main stem were recorded for each individual plant. Tillers were not separated and their mass was considered jointly in the plant mass. The projected area of leaves and stems were determined with an area meter (AT Delta-T). The plants were then oven-dried at 70 °C for 48 h before determining the dry mass of each individual leaf and of the stem.

Growth chamber experiments

The relationships between seed size and seedling development was also studied in growth chambers, at high and low temperatures (22/12 °C, and 15/5 °C day/night temperatures, respectively), with a photoperiod of 8 h. Photosynthetically active radiation (PAR) was 100 μmol/m²/s. Seeds of each genotype were divided into three grading sizes, according to their diameter: large (2·8–3·5 mm), medium (2·2–2·5 mm) and small (1·8–2·2 mm). The seeds were placed in trays of 28 square cells, each of 6·2 cm width and 6 cm height. One seed was sown in each cell at the same depth (3 cm), using the same potting mix as in the glasshouse experiment. Each experimental plot consisted of four cells. A randomized block design with three replicates was used for each temperature, with the 12 combinations of the four genotypes and three seed sizes randomized within replicate blocks within each growth chamber. All plots were well watered during the experiment, and the position of the trays in the growth chamber was periodically moved during the experiment to reduce any environmental effects on growth.

Thermal time was calculated as in the glasshouse experiment. The following variables were determined from data recorded every second day on each plant: thermal duration from sowing to plant emergence (GDD), thermal duration from plant emergence to the complete extension of the first leaf (GDD), and rate of leaf appearance for the first two leaves, and for the third and fourth leaves (number of leaves/GDD).

Statistical analyses

The data were analysed using conventional analysis of variance (ANOVA). *F*-values were the criteria used to assess which of the morphological, developmental and biomass traits were most affected by seed-grading size. Correlation and regression techniques were also used. All statistical analyses were carried out using standard SAS-STAT procedures (SAS Institute Inc. 1987).

RESULTS

Relationship between seed size and seed morphology

Morphological characteristics were determined in seeds of the three grading sizes used in the glasshouse experiment. There were significant differences among the three seed-sizes for all the traits evaluated (Table 1). *F*-values of the analyses of variance for seed and embryo areas were higher than the values for the other measured morphological characteristics (Table 1), and this suggests that these traits were the ones most strongly affected by changing seed-grading size. The correlation coefficient between the area of the seed and the area of the embryo for the 24 data pairs arising from the 24 combinations between genotypes and grading sizes was strongly significant ($r = 0{\cdot}98$, $P < 0{\cdot}001$).

Seedling development

The three growth rates used to measure the development of seedlings in the glasshouse depended on seed size and genotype. The thermal time from sowing to plant emergence decreased steadily and approximately linearly as the seed size increased (Table 2). Similarly, the rate of first-leaf growth and the rate of appearance of the first four leaves increased steadily and approximately linearly as the seed size increased.

The *F*-values of the analysis of variance for the seed size effect were significant ($P < 0{\cdot}001$) for the three traits studied, the thermal duration to plant emergence, the rate of first-leaf growth and the mean rate of appearance of leaves 1 to 4. These results show that in the glasshouse experiments, the rate of first-leaf growth was the seedling developmental trait most affected by seed size (Table 2).

Given the lack of true replication for water regime and temperature treatments, significance tests for the main effects of these treatments were not available. However, the simple treatment mean comparisons suggest that under daily irrigation the seeds took more time to germinate, and the rate of growth of the first leaf was lower than under irrigation every third day (Table 2). Differences between genotypes were statistically significant for the three developmental traits studied. Sebah, Awalbit, Omrabi-3 and Korifla were the genotypes that emerged latest, and these had generally lower rates of growth of the first leaf and lower rate of appearance of the first four leaves than most of the genotypes that emerged earlier. The interaction genotype × seed size was not significant for the thermal duration to plant emergence, but it was statistically significant for the mean rate of appearance of leaves 1 to 4 ($P < 0{\cdot}01$) and for the rate of first-leaf growth ($P < 0{\cdot}05$). However, it was a non-cross-over interaction for both traits, since the two increased steadily with seed size in all genotypes, without changing the rank of seed sizes. Other interactions were not significant in most cases, and when significant they were non-cross-over interactions.

Results of the growth chamber experiments showed that temperature affected the development of the plant up until about the fourth-leaf stage (Table 3). Germination and seedling development were accelerated at high temperature, regardless of seed size. A significant ($P < 0{\cdot}05$) non-cross-over interaction was observed between seed size and temperature for the rate of leaf appearance of the first two leaves, since the high temperature increased the differences between large and medium and small seeds in the rate of appearance of the first two leaves (data not shown).

Under growth chamber conditions, the time required for the emergence of the plants was similar

Table 1. *Seed and embryo traits for the three seed sizes used in glasshouse experiments. Data are means over eight genotypes and five replicate determinations for each genotype and seed size*

Trait	R^2 of ANOVA for seed size	F value for seed size effect	Seed size Small	Medium	Large	S.E.†
Seed						
Mass (mg)			15·8	29·8	61·8	0·67
Length (mm)	0·90	58·8***	6·43	6·85	8·23	0·123
Area (mm²)	0·97	231·7***	12·45	15·24	25·56	0·454
Perimeter (mm)	0·94	104·3***	15·81	16·94	20·97	0·266
Embryo						
Length (mm)	0·94	106·1***	1·87	2·16	2·80	0·046
Width (mm)	0·95	122·4***	0·68	0·79	1·12	0·020
Area (mm²)	0·97	223·8***	1·12	1·45	2·70	0·056
Perimeter (mm)	0·95	137·8***	5·00	5·89	7·59	0·112

† S.E. with 14 D.F.; *** $P < 0·001$.

Table 2. *Seedling developmental rates for each water regime, seed size and genotype in glasshouse experiments*

Factor	Treatment	Thermal duration to plant emergence (GDD)	Rate of first-leaf growth (mg /GDD)	Mean rate of appearance of leaves 1 to 4 (leaves/GDD)
Water regime ($n = 96$)	Daily irrigation	159	0·038	0·0074
	Irrigation every third day	77	0·054	0·0070
Seed size ($n = 64$)	Small	122	0·029	0·0068
	Medium	118	0·047	0·0072
	Large	115	0·063	0·0076
	S.E.†	1·04	0·0016	0·00004
Genotype ($n = 24$)	Altar-Aos	115	0·054	0·0068
	Mexa	113	0·045	0·0073
	Vitrón	116	0·048	0·0075
	Jabato	116	0·047	0·0075
	Korifla	120	0·045	0·0073
	Omrabi-3	121	0·044	0·0070
	Sebah	124	0·041	0·0070
	Awalbit	121	0·045	0·0072
	S.E.†	1·69	0·0026	0·00007

† S.E. based on a pooled error term with 138 D.F.

for the three seed sizes considered, but the development of the first leaf took more time for small seeds than for medium or large seeds. The rate of leaf appearance of the first two leaves was significantly associated with seed size, whereas the rate of leaf appearance of leaves 3 and 4 was not (Table 3).

The relationship between seed size and morphology and the rate of development of the young plants was further studied by means of regression analysis. Under glasshouse conditions the three seedling developmental rates strongly depended on embryo size (Table 4). However, under growth chamber conditions the percentage of variance explained by seed and embryo traits was much lower than it was in the glasshouse experiment, and no significant relationship was found for the thermal duration to plant emergence and the mean rate of leaf appearance of leaves 3 and 4.

Seedling biomass

The relative influence of the different sources of variation on the 23 biomass traits listed in Table 5 and evaluated in seedlings in the glasshouse was tested by means of analysis of variance (data not shown). The traits measured on the first four leaves were similar for both water regimes, except for the area of leaves

Table 3. *Seedling developmental rates for each temperature, seed size and genotype in growth chamber experiments*

Factor	Treatment	Thermal duration to plant emergence (GDD)	Thermal duration from plant emergence to the complete development of the first leaf (GDD)	Mean rate of leaf appearance of leaves 1 and 2 (leaves/GDD)	Mean rate of leaf appearance of leaves 3 and 4 (leaves/GDD)
Temperature ($n = 36$)	High	81·0	66·2	0·0053	0·0053
	Low	98·6	78·9	0·0071	0·0057
Seed size ($n = 24$)	Small	88·4	95·9	0·0058	0·0054
	Medium	91·7	86·7	0·0061	0·0055
	Large	89·3	76·5	0·0086	0·0056
	S.E.†	1·86	2·05	0·00028	0·00012
Genotype ($n = 18$)	Altar-Aos	92·4	91·0	0·0052	0·0056
	Jabato	86·6	86·7	0·0066	0·0053
	Sebah	90·6	84·9	0·0059	0·0057
	Vitrón	89·7	88·0	0·0070	0·0054
	S.E.†	2·15	2·37	0·00033	0·00013

† S.E. based on a pooled error term with 44 D.F.

Table 4. *Linear regression equations for the relationship between seedling developmental rates and seed and embryo traits in glasshouse and growth chamber experiments.* S.E. *of the coefficients are between parentheses*

Seedling developmental rate (y)	Significant equation ($P < 0·05$)	Model R^2
	Glasshouse (eight genotypes)	
Thermal duration to plant emergence	$y = 133·10 - 17·2 \times$ Embryo width (3·83) (4·33)	0·42
Rate of first-leaf growth	$y = -0·0307 + 0·0125 \times$ Embryo perimeter (0·0080) (0·0013)	0·81
Mean rate of appearance of leaves 1 to 4	$y = 0·00583 + 0·0016 \times$ Embryo width (0·00025) (0·00029)	0·58
	Growth chamber (four genotypes)	
Thermal duration to plant emergence	None	—
Thermal duration from plant emergence to the complete development of the first leaf	$y = 152·06 - 8·99 \times$ Seed length (17·50) (2·43)	0·19
Mean rate of leaf appearance of leaves 1 and 2	$y = 0·0101 - 0·00296 \times$ Embryo perimeter $+ 0·00082 \times$ Seed area (0·00397) (0·00126) (0·00023)	0·49
Mean rate of leaf appearance of leaves 3 and 4	None	—

1 to 3, which was higher for irrigation every third day than for daily irrigation. However, this pattern was later reversed. Thus, the areas of leaves 5 and 6 were higher when irrigation was provided daily. In addition, dry mass of leaves 5 and 6 as well as length, areas and mass of the stem at this stage were higher under full irrigation conditions.

Overall, the factor accounting for most of the variation was seed size, the effect of which was highly significant for all the traits measured (Table 5). Large seeds gave plants with a higher biomass than medium seeds which, in turn, gave plants with a higher biomass than small seeds. Correlation coefficients between seed mass and the seed morphological traits and the 23 biomass traits evaluated under glasshouse conditions were positive and significant in all cases (data not shown). Small seeds gave plants with shorter and narrower leaves and stems, and consequently with less leaf area and mass.

Sebah, Omrabi-3 and Awalbit had the widest first leaves within the range of seed sizes considered in this study (Table 6). The four genotypes included in the growth chamber experiment differed significantly only in the rate of appearance of the first two leaves (Table 3). Genotypes differed significantly for most of the biomass traits analysed on individual leaves, but not

Table 5. *Biomass traits for the three seed sizes in glasshouse experiments*

Trait	F value for seed size effect	Seed size Small	Medium	Large	S.E. (138 D.F.) ($n = 64$)
First leaf					
Length (cm)	138·7***	11·0	12·1	13·1	0·09
Width (cm)	262·6***	0·33	0·44	0·49	0·005
Area (cm²)	449·3***	2·27	3·51	4·84	0·06
Mass (mg)	107·6***	6·0	9·1	11·5	0·27
Second leaf					
Length (cm)	184·5***	16·1	17·3	18·9	0·10
Width (cm)	192·3***	0·33	0·44	0·51	0·006
Area (cm²)	269·3***	3·2	4·4	6·3	0·09
Mass (mg)	70·4***	7·7	11·2	13·5	0·34
Third leaf					
Length (cm)	361·1***	21·7	23·7	26·5	0·13
Width (cm)	38·0***	0·56	0·60	0·64	0·006
Area (cm²)	303·3***	7·9	9·6	11·8	0·11
Mass (mg)	29·6***	16·8	21·3	24·2	0·68
Fourth leaf					
Length (cm)	200·5***	25·1	26·9	28·2	0·11
Width (cm)	135·1***	0·75	0·83	0·88	0·006
Area (cm²)	253·1***	12·9	15·6	18·3	0·17
Mass (mg)	43·0***	28·2	35·3	38·7	0·82
Leaves 5 and 6					
Area (cm²)	109·8***	7·9	16·4	22·1	0·69
Mass (mg)	91·5***	20·5	43·7	56·7	1·94
Stem					
Length (cm)	123·9***	14·0	15·3	16·7	0·12
Area (cm²)	132·7***	3·5	4·6	5·5	0·09
Mass (mg)	61·4***	51·4	75·1	88·5	2·39
Whole seedling					
Mass (mg)	149·2***	130	196	245	4·5
Leaf area (cm²)	245·3***	34·3	49·6	63·4	0·93

*** $P < 0{\cdot}001$.

Table 6. *Width of the first leaf and whole seedling mass and leaf area at fourth-leaf stage, for the eight genotypes in glasshouse experiments*

Genotype	Width of the first leaf (cm)	Seedling mass (mg)	Seedling leaf area (cm²)
Altar-Aos	0·42	194	48·5
Mexa	0·42	193	48·7
Vitrón	0·40	192	49·8
Jabato	0·40	179	48·9
Korifla	0·42	187	47·1
Omrabi-3	0·43	188	49·6
Sebah	0·43	178	46·7
Awalbit	0·44	200	52·7
S.E. (138 D.F.) ($n = 24$)	0·008	7·4	1·52

for stem area and mass (data not shown) or for total plant mass (Table 6). Interactions between genotype and seed size were significant for many of the traits studied.

According to the F-values of the analyses of variance, the area of the first leaf was the biomass trait most strongly affected by seed-size (Table 5). The relationships between the embryo perimeter and the

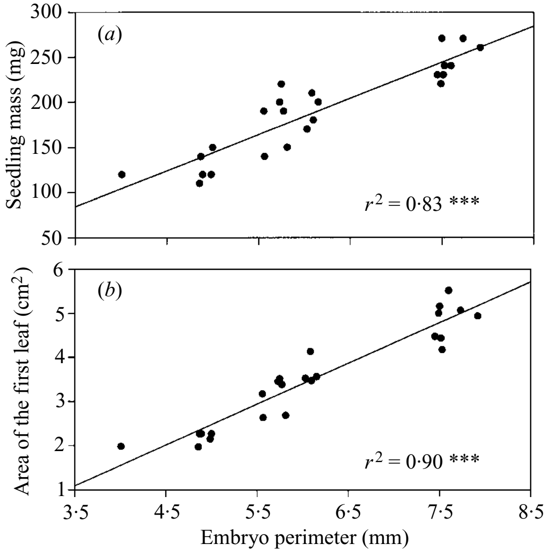

Fig. 1. Relationship between embryo perimeter and (*a*) seedling mass at the fourth-leaf stage and (*b*) area of the first leaf in glasshouse experiments. Points represent all combinations of eight genotypes and three seed sizes ($n = 24$).

area of the first leaf and the seedling mass are shown in Fig. 1*a* and 1*b* respectively.

DISCUSSION

Relationship between seed size and seed morphology

A strong relationship was found between the size of the seed and all the morphological traits of the seed and the embryo considered in this study. Not only were the mass, length, sectional area and perimeter of the seed strongly positively related to the seed grading size, but also the length, width, area and perimeter of the embryo.

The results of the statistical analysis indicated that the area of the seed and the area of the embryo were the seed traits more influenced by changing seed grading size. However, since the two variables were strongly correlated, it was not possible to separate their relative contribution to the development and growth of seedlings.

Seedling development

Germination took more time and the growth rate of the first leaf was lower under daily irrigation than under irrigation every third day. However, the rate of appearance of the first four leaves of the plant was greater when irrigation was provided daily. Two possible hypotheses may be argued to explain these results: lower soil temperatures and/or temporarily anaerobic conditions during germination and plant emergence could have occurred when irrigation was provided daily. These hypotheses are also supported by the observed effect of water status on the area of the first three leaves, which was higher under water-limited conditions. However, daily irrigation was more favourable for the development of plant structures produced later, such as leaves 5 and 6 and stems, leading to heavier plants with greater leaf area.

The development of the first leaf and the mean rate of appearance of the first four leaves were strongly associated with seed size. However, when a two-phase development of seedling leaves was considered, and the rate of leaf appearance of the first two leaves was studied separately from the rate of appearance of the subsequent two, evidence was obtained of the association of seed size only with the development of the first two leaves, since thereafter seedling development rates were similar for all treatments, regardless of seed size. It is well known that until the complete expansion of the first two leaves of wheat, seedlings utilize seed reserves, whereas after this time the principal energy source is photosynthate from emerged leaves (Peterson *et al.* 1989).

The results of the statistical analysis of the three developmental traits studied under glasshouse conditions showed that seed size affected the rate of growth of the first leaf more than the mean rate of appearance of leaves 1 to 4 or the thermal duration to plant emergence. This result supports the hypothesis that there is a large influence of environment on the duration of plant emergence (Kirby *et al.* 1985; Kirby & Perry 1987).

Seedling biomass

Results on the effect of seed size on the biomass attained by seedlings support other studies that show a positive relationship between seed size and seedling growth in wheat and other cereals (Bremner *et al.* 1963; Bishnoi & Sapra 1975; Evans & Bhatt 1977; Halloran & Pennell 1982; Peterson *et al.* 1989).

Among the 23 biomass traits studied the area of the first leaf was the most affected by seed size. In a previous study in bread wheat, Peterson *et al.* (1989) suggested a positive relationship between seed size and the growth of the first two leaves; this relationship then had an influence on the growth of the subsequent leaves.

Genotypic differences

The eight genotypes used in the glasshouse experiment showed differences in early development. The genotypes Sebah, Awalbit and Omrabi-3 emerged later than the other genotypes and had lower values for the rate of growth of the first leaf and for the mean rate of leaf appearance of leaves 1 to 4. Nevertheless, they had the widest first leaves. Lafond & Baker (1986) also observed that the seeds that emerged most quickly led to plants that accumulated least dry matter, but in their study this effect was related to seeds of small size. Differences appeared between the four genotypes used in the growth chamber experiment for leaf biomass traits, but not for stem measured traits. Genetic variability for early vigour has been reported in other temperate cereals (Turner & Nicolas 1987; Richards 1987, 1996; Regan *et al.* 1992).

CONCLUDING REMARKS

Our results demonstrate the important relationship existing between seed size and early growth and development of durum wheat. The rate of growth of the first leaf and the area of the first leaf were the developmental and growth traits respectively, most affected by changing seed-grading size. Among the seed morphological traits, the area of the seed and the area of the embryo were the most influenced by seed size. However, the strong correlation existing between these two traits meant that the relative contribution of the two traits to the development and growth of durum wheat could not be determined on the basis of the data set obtained in this study.

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