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Genetic resources and selection methods for drought and salinity resistance in durum wheat

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GENETIC RESOURCES AND SELECTION METHODS FOR DROUGHT AND SALINITY RESISTANCE IN DURUM WHEAT

A dissertation presented in partial fulfilment of the
requirements for the degree of Doctor of Philosophy
in Biological Sciences of the University of Wales

by

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SUMMARY

The relevance of drought and salinity stress under Mediterranean conditions is reviewed and prospects for crop improvement against these constraints are discussed.

Field trials under severe drought in Syria highlighted the importance of earliness to ensure satisfactory yields. Peduncle length and frost tolerance were also important attributes. Under more favourable conditions in Sicily, the yield components *per se* (number of spikes, number of kernels and kernel weight) had greater influence on genotype performance. At both locations of evaluation high yields were attained through different architectures of traits.

Durum wheat genetic resources proved very variable. Genotypes were identified which could be used as donors of adaptive characters in breeding programmes.

The CERES-Wheat growth model was used for the two locations, using historical weather data and two genotypes of known adaptation to the region. Early heading was a positive attribute, particularly in Syria. At both sites, lengthening of the grain filling period resulted in higher yields. Three sowing dates were simulated. "Early" sowing (1 November) had the highest simulated yield in both environments, suggesting a possible agronomic means to improve yields under stress. Simulated yields were in most cases within 15% of measured values when a comparison was possible.

The ability to adjust osmotically was sought in seedlings artificially exposed to drought stress during early development. One entry appeared to possess this feature. However, another genotype, of known tolerance under real conditions, did not show this ability. Therefore, osmotic adjustment during early stages of ontogeny does not seem unequivocally able to identify the best genotypes under drought.

Salt tolerance of durum wheat genetic resources was assessed measuring early growth under controlled environment. The data indicated that the results may be somewhat experiment-specific when using different growing techniques such as hydroponics and sand-culture. Finding tolerant tetraploid entries in terms of plant survival and ion uptake seemed difficult. However, variability existed and some entries, less susceptible than others, were noted. They could be used for breeding. For instance, they could be valuable recipient for the introgression of identified resistance mechanisms from other taxa.

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1.1 *Durum wheat*

Durum wheat (*Triticum turgidum* (L.) Thell. ssp. *turgidum* conv. *durum* (Desf.) MacKey) (syn. *T. durum* Desf. and *T. turgidum* L.) is a tetraploid ($2n=4x=28$) member of the subtribe *Triticinae*, tribe *Triticeae*, family *Gramineae* (=*Poaceae*). By genome analysis, i.e., the study of the chromosome pairing at meiosis in crosses between related taxa, this species appeared to be an amphipolyploid bearing the genome indicated as AABB (Kimber and Sears, 1983). This possibly originated from chromosome doubling following the hybridisation between a diploid einkorn wheat (*Triticum monococcum* L. *sensu lato*, genome AA) and some unknown donor species of the diploid genome presently designated as BB. However, some differentiation in the A genome of *T. turgidum* relative to that in the diploid has been indicated (Miller and Reader, 1980). There is not yet agreement among geneticists and cytogeneticists on which *Aegilops* species is the donor of the B genome of the tetraploid and hexaploid wheats. It was suggested (Riley *et al.*, 1958) that *Aegilops speltoides* Tausch was the B-donor species. More recently *Ae. sharonensis* Eig was proposed as the donor of the B genome (Kushnir and Halloran, 1981), whereas *Ae. speltoides* could be considered the donor of the G genome of the tetraploid *T. timopheevi* Zhuk. (genome AAGG) (Boggini *et al.*, 1989). It is likely that more than one amphidiploid originated, having in common only the genome A which ensured a certain level of interfertility and exchange of genetic material. From these ancestral amphidiploids the present types evolved, no longer having an exact relationship with the diploids originally involved in the polyploidisation process. Suemoto (1973) demonstrated that the B genome donor contributed to the cytoplasm of durum wheat, and was presumably the female parent. Therefore, as the female parent has to be written first in a cross notation, the genome formula of durum wheat should be indicated as BBAA instead of AABB (Waines and Barnhart, 1990).

Archeological findings show that emmer (*Triticum dicoccum* Schlub.) was the dominant wheat in the Fertile Crescent of the near east since the early Neolithic and remained as such throughout the Neolithic dispersal across Europe and north Africa during some millennia B.C. (a thorough literature review was compiled by Harlan (1981)). Archeological evidence exists that naked wheats were also available from the early Neolithic. They have usually been classified by archeobotanists as the hexaploid *T. aestivum* (L. em. Thell.). However, Harlan (1981) argued that when dealing with small numbers of poorly preserved materials, extreme taxonomic caution is necessary. Van Zeist (1976) concluded that it is not possible to separate hexaploid and tetraploid naked wheats on the basis of carbonised grains, rachis forks or other plant parts found in archeological sites. Following this statement and some considerations relative to the distribution of durum wheat, Harlan (1981) was "tempted" to ascribe all the early traces of naked wheats from the Mediterranean and the near east to the tetraploid group. Harlan (1981) concluded that "the durums are Mediterranean in adaptation and diminish in diversity and performance as they are removed from the region".

Vavilov (1951) considered the near east, the Mediterranean and Ethiopia as the centres of diversification of this crop. For centuries durum wheat had experienced many natural conditions and management practices, spreading from east to west (Ciferri and Bonvicini, 1960; Porceddu, 1979) following the migrations of peoples, resulting in different combinations of characters occurring in different places. At the turn of this century, a great diversity of forms was found in Algeria and Egypt (Orlov, 1923, cited in (Harlan, 1981)), while there were a number of races endemic to Ethiopia (Vavilov, 1926, cited in (Harlan, 1981)). In the rest of the Old World, a great diversity existed in both durum and bread wheat in India (Howard and Howard, 1927, cited in (Harlan, 1981)) whereas almost all the wheats of the far east were (and are) hexaploid. In recent years, evaluations of world durum wheat germplasm collections have revealed considerable phenotypic diversity in materials from Ethiopia, the Mediterranean and India for a set of six morphological traits (Jain *et al.*, 1975), from Italy for six agronomic characters (Porceddu, 1976), and from India, Egypt, Tunisia, Ethiopia, Italy and USA for seven morpho-physiological traits (Pecetti *et al.*, 1992a). On the basis of isoenzymatic characters, the greatest variation was found by Asins and Carbonell (1989) in durum wheat from Iran, Mexico, Ethiopia, Egypt and Afghanistan. It is interesting that, besides country gene pools historically reported as rich in variation, new 'centres of diversity' (using this term in the sense indicated by Peeters (1988)) are emerging, mainly because of the intensive breeding activity which has been carried out during the last decades (and is still going on) in certain countries. Confirming the above-mentioned observations by Harlan (1981), materials originating from the Mediterranean basin show great variation and appear generally well adapted to the conditions prevailing in this area (Jana *et al.*, 1990; Pecetti and Annicchiarico, 1991).

1.1.1 *West Asia and north Africa*

At the beginning of the 1980's, durum wheat covered approximately 8% of the 240 million hectares under wheat cultivation in the world (Srivastava, 1984). Its distribution is mainly concentrated in the Mediterranean basin (Figure 1) where about 75% of world consumption also occurs. Countries in west Asia and north

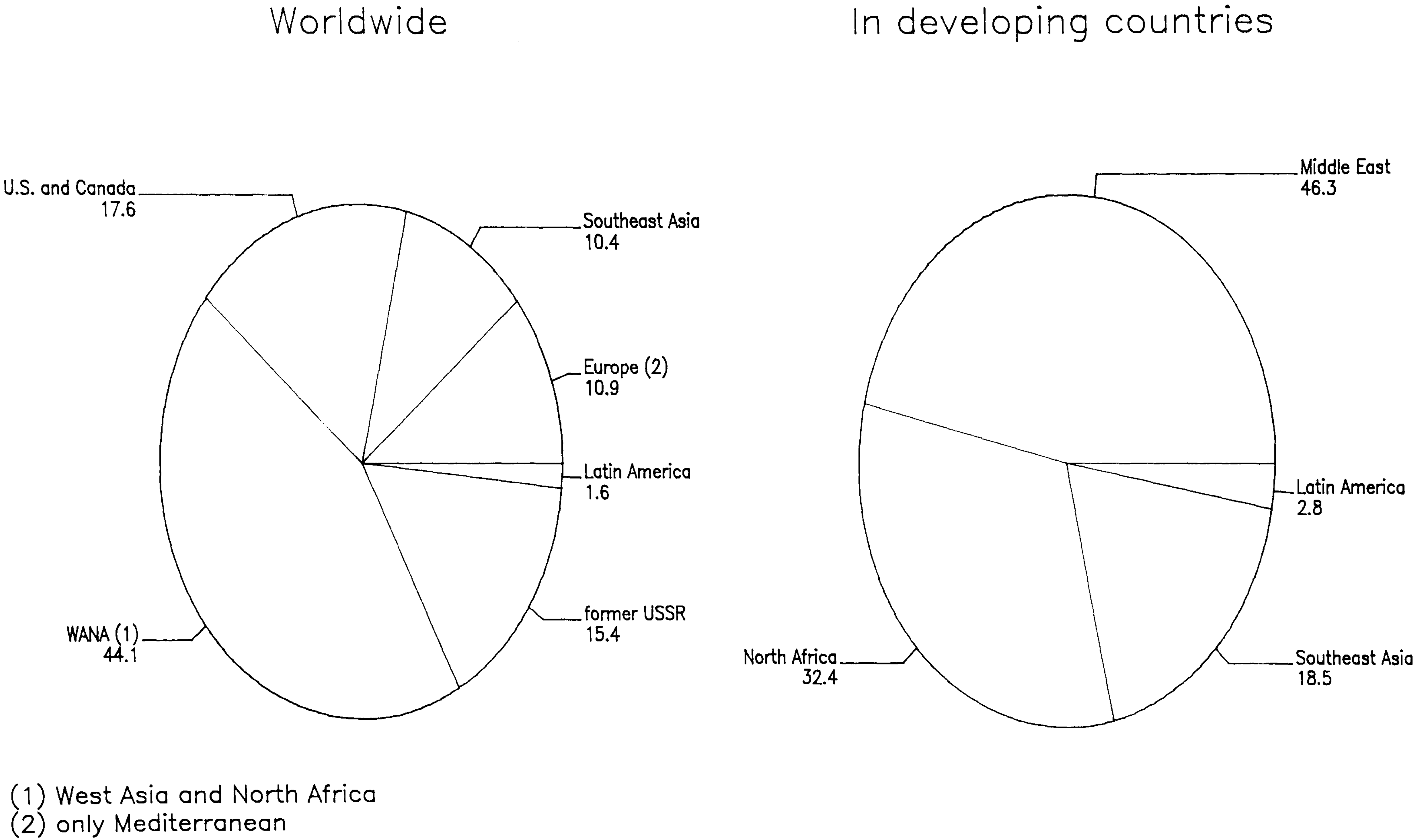


Figure 1. World distribution (% area) of durum wheat. From: Srivastava (1984).

Africa (WANA) account for about 80% of the durum wheat grown in developing countries. This crop occupies in most cases at least two thirds of the national total area of all wheat (Srivastava, 1984). Nearly 50% of durum wheat is consumed in WANA in the form of baked products, mainly single and two-layered flat breads. Other important durum-derived foods are represented by cous-cous, pasta products, burghul and frekeh (Williams *et al.*, 1990). In WANA durum wheat is the second crop in acreage after barley, being cultivated on approximately 8.6 million hectares, of which about 98% are under rainfed conditions. About 4.7 million hectares are situated in the low-rainfall zones, receiving less than 400 mm per year. The average grain yield is about 1000 kg ha^{-1} in the high rainfall areas (>400 mm) and 600 kg ha^{-1} in the low-rainfall areas. Both these figures are about 30% lower than those for bread wheat in the region (ICARDA, 1985). Detailed information on the agroclimatic conditions under which durum wheat is grown in WANA are reported in Table 1. Compared to bread wheat, durum wheat is mostly restricted to the drier and less favourable growing conditions, and under generally poor farm management practices. Altogether, these factors account for the mentioned difference between the average yields of durum and hexaploid wheats. The average consumption in WANA ranges between 150 and 200 kg per person per year (Nachit, 1988), and the demand is growing. Despite the importance of this crop in the human diet, the improvement of durum wheat yield in WANA, although it shows a modest increase, has been far outpaced by both that of bread wheat in the same region and that of durum wheat in Mediterranean Europe (Srivastava, 1984).

The low productivity of the crop in the region is due to several environmental and socio-economic causes. The former include the frequent occurrence and the erratic seasonal variation of abiotic (drought, low winter temperature, late frosts, high temperatures during the grain filling, saline soils) and biotic (grain and foliar pathogens, insect pests) stresses. Among the abiotic stresses, drought

Table 1. Agroclimatic conditions under which durum wheat is grown in west Asia and north Africa. From: Srivastava (1984).

Country	Precipitation (mm)		Type of agriculture (%) T = traditional M = modern	Rainfed (R) or irrigated (I) (%)	Yield (kg ha^{-1})
	Range	Mean			
Afghanistan	250-500	350	T = 100	R = 50 I = 50	1100
Algeria	300-700	500	T = 70 M = 30	R = 100	620
Cyprus	100-450	300	T = 5 M = 95	R = 90 I = 10	1130
Iraq	300-700	400	T = 80 M = 20	R = 100	1130
Jordan	250-400	350	T = 95 M = 5	R = 95 I = 5	740
Libya	na	300	na	R = 100	550
Morocco	250-650	400	T = 75 M = 25	R = 96 I = 4	1000
Syria	250-450	350	T = 65 M = 35	R = 95 I = 5	900
Tunisia	200-700	400	T = 70 M = 30	R = 100	700
Turkey (Central Plateau)	275-600	350	T = 80 M = 20	R = 100	1100
Turkey (Southeast)	300-600	480	T = 60 M = 40	R = 99 I = 1	1050
Ethiopia	400-1000	750	T = 90 M = 10	R = 100	700

na: not available.

stress is of paramount importance, as it occurs with severe incidence in about 70% of the durum wheat growing area in WANA (Table 2).

1.1.2 *Sicily*

Of the about 2.8 million ha devoted to durum wheat in the EU, 66.6% are situated in Italy and correspond to 65.7% of the total annual production of about 5.9 million t. The average crop yield in Italy is 2.39 t ha^{-1}, similar to that obtained in Greece (2.38 t ha^{-1}), higher than that in Spain and Portugal (respectively 1.94 and 1.43 t ha^{-1}), and lower than that in France (3.98 t ha^{-1}). Italy has a long-standing tradition of durum wheat growing and of pasta-product utilisation. The average consumption per capitum per year of pasta in the country is 25 kg (more than double that of the following country in the world ranking), with a peak of 43 kg in southern Italy (Boggini and Lombardo, 1992). Durum wheat is, therefore, a major food crop in Italy, and in this panorama Sicily occupies a leading position. Indeed, 31% of the total national growing area and 25.6% of the national production come from this island. Durum wheat in Sicily covers 46% of the total sown area and 21% of the total agricultural surface, representing 96% of the total winter cereal cultivation. While in the rest of Italy the surface devoted to durum wheat has increased during the last 30 years (mainly due to the selection of varieties suited to the conditions of central and, even, northern Italy), in Sicily during the same period about 100 thousand ha (15.4%) of the crop have been abandoned. The main reason for such contraction is the tendency by farmers to give up lands that, because of their location (mainly their slope) and their pedoclimatic characteristics, are no longer cost-effective for durum wheat growing. A proportion of 72.1% of the crop area lies in the hilly inner part of the island, 18.4% is mountai-

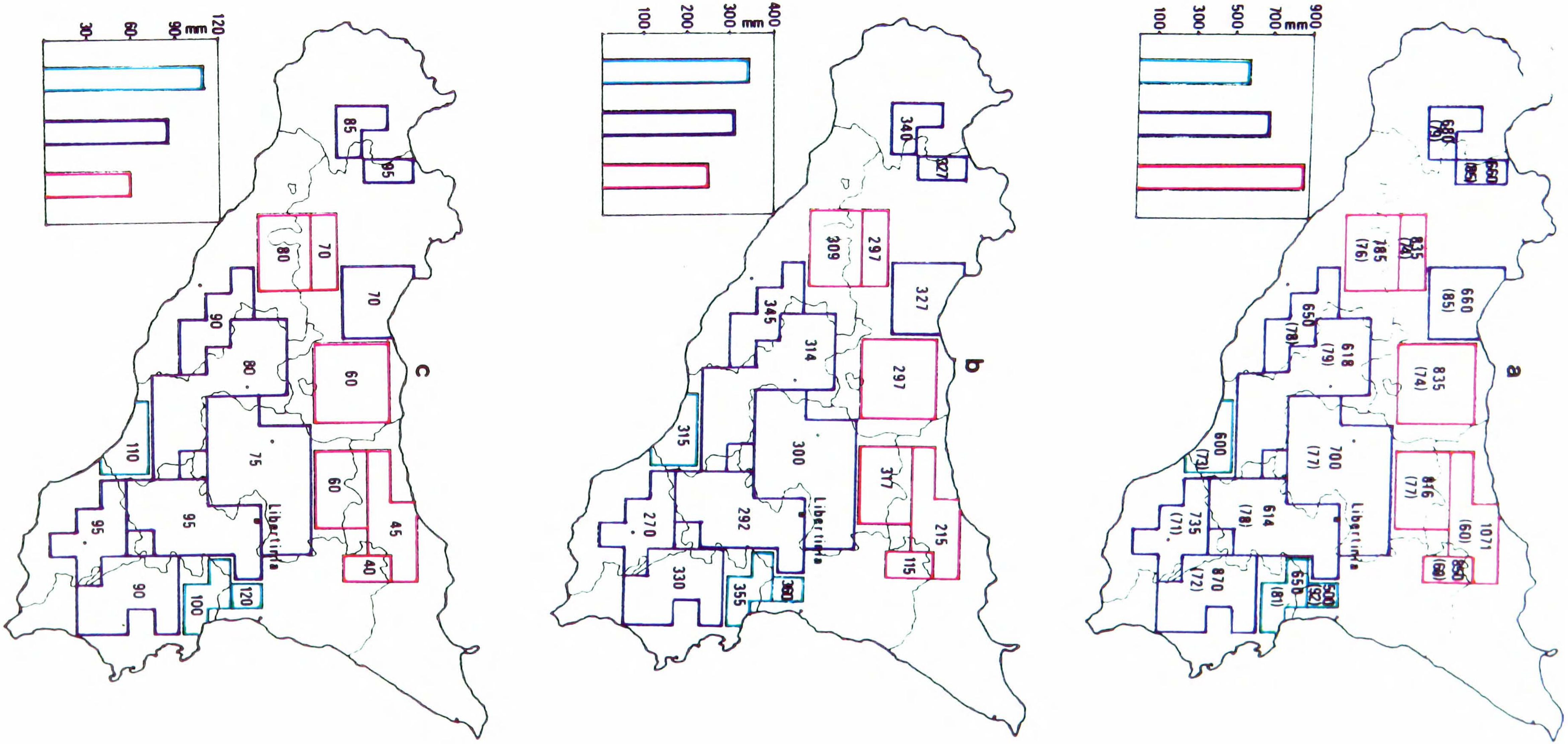
Table 2. Area and average grain yield of durum wheat under different moisture regimes in west Asia and north Africa. From: Nachit (1988).

Moisture regime	Area (x1000)		Grain yield
	ha	%	(t ha^{-1})
Usually under some stress	3500	41	0.63
Frequently stressed	2400	27	0.98
Sometimes stressed	2500	29	1.23
Rarely stressed	500	3	2.12

nous, and only 9.5% is in lowlands (Figure 2). The pedoclimatic conditions of these areas are generally unfavourable. Most of the soils are Regosols developed from clay rocks, with grey colour (from light to dark) and depth varying from 10-15 cm to 70-80 cm where the erosion is limited. However, their slope is more or less accentuated and, therefore, they are very subject to strong erosion. These soils are usually clayey or clay-calcareous, with pH sub-alkaline or alkaline. The content of potassium is generally good, while organic matter, phosphorus and nitrogen are present in lower quantities. The productive potential of these Regosols is considered low (Fierotti *et al.*, 1988).

Rainfall in Sicily is distributed erratically within and among seasons, being typical of a Mediterranean climate. The long-term average for the three cropping zones, viz., lowlands (up to 200 m above the sea level (asl)), hills (up to 600 m asl) and mountains, is about 580 mm, 690 mm and 780 mm, respectively (Figure 2a). However, given the uneven distribution of rainfall during the season, there are periods of water surplus, followed by periods of water deficit. The former occur more frequently between November and March, when rainfall exceeds the evapo-transpiration. The surplus is the amount of water which is lost by run-off and, after soil saturation, deep drainage. Therefore the amount of water effectively available for the crop is the difference between the rainfall and the water surplus in the same period. For the above-mentioned three zones it corresponds, on average, to 343 mm, 314 mm and 250 mm, respectively (Figure 2b). It is noteworthy that, on average, 70-80% of the total annual rains fall between October and March (Figure 2a). The water deficit becomes evident from May onwards, being estimated (as difference between effective and potential evapo-transpiration) at between 60 mm and 110 mm for the three zones in May and June, i.e., during the grain filling period of the crop (Figure 2c). Such a rainfall regime is very unfavourable for winter cereals, as abundant rains in autumn-winter favour a shallow distribution of roots which are not able later to reach deeply stored water when the dry

Figure 2. Different moisture parameters shown for the main durum wheat growing areas in Sicily: lowlands (≤ 200 m asl, in green), hilly areas (200-600 m asl, in blue) and mountainous areas (> 600 m asl, in red); a) total annual (September-August) rainfall (mm) and rainfall percentage between October and March (in parentheses); b) effectively available water (mm) between October and March; c) water deficit (mm) in the period May-June. In the three boxes are shown the average values for the three cropping zones. All figures are 30-year means (1921-1950). From: Foti *et al.* (1988).



season begins. The stressful conditions in late-spring are often accentuated by the sharp rise of temperatures caused by the 'Scirocco', i.e., a hot wind from the Libyan deserts. Evapo-transpiration demands increase drastically under the effect of the wind and are not compensated by a proportional increase in water use by the crop. It is not rare that in just one day of Scirocco during the grain filling period all the kernels are subject to the so-called 'stretta' (=shrivelling), resulting in a crop failure.

The farming system adopted in the durum wheat growing areas is traditionally low-input and sustainable (not from an up-to-date choice but from economic need), with limited nitrogen supply, limited chemical weed control and no pest or pathogen control. The use of non-certified seed or the adoption of continuous wheat growing are still very common practices.

In the face of this complex of unfavourable conditions, durum wheat breeding has not achieved dramatic results. While the overall average yield per hectare in overall Italy has increased by 110% between 1955 and 1985, during the same period the increase in Sicily has been 55%, passing from 1.12 to 1.74 t ha^{-1} (Foti *et al.*, 1988). High-yielding varieties have recently spread in central and northern Italy (Porceddu, 1987), while in Sicily the 40-year-old cultivar 'Capeiti' still covers 38% of the total area, and some local landraces already cultivated at the turn of the century are still grown, particularly in the mountainous areas (Boggini *et al.*, 1990). The reason for the choice of cultivars of low potential is to be found in their better adaptability to the difficult growing conditions of the island, ensuring fair stability of production (the role of landraces and old cultivars under these conditions will be developed in section 1.4). The stagnation of yields in the less favourable areas of Italy during the last few decades (Annicchiarico and Pecetti, 1988; Foti *et al.*, 1988) is also related to the narrow genetic base of the more recently bred durum wheat varieties (Boggini *et al.*, 1992). Given the existing situation, there is great scope for breeding durum wheat in Sicily to improve its yield and yield stability, in particular introducing from the Mediterranean basin sources of adaptation to the prevailing agro-pedo-climatic conditions in the island.

1.2 *Drought*

"Drought" is a comparative rather than an exact term indicating a meteorological and hydrological event which involves precipitation, evaporation and soil water storage (McWilliam, 1986). Meteorological drought occurs when the precipitation over a certain area for an extended period is significantly lower than the long-term average. Agricultural drought is said to exist when the level and distribution of precipitation is sufficiently poor to cause serious shortfalls in crop yields. Drought remains the single most important factor threatening the food security of people in the developing world. An insidious and widespread problem is the extension of agriculture into more fragile marginal lands under an ever-increasing population pressure. These areas are marginal either because of their geographic position (in semi-arid environments) or because of their characteristics (often hilly; very often with shallow, eroded soil and poor water-holding capacity) (McWilliam, 1989). Drought is, therefore, a natural phenomenon whose impact and severity are exacerbated by the activities of Man.

Drought limits the time during the year when plant growth can occur, and often limits the rate of growth during the growing season, so setting upper limits to crop yields. In dry environments, variation in rainfall (or water supply to the crop) can account for most of the variation in yield (Austin, 1989; Pecetti and Annicchiarico, 1993).

The water deficit of a plant begins when the evaporative demand of the atmosphere upon the leaves (potential transpiration) exceeds the capacity of the roots to extract water from the soil (actual transpiration). Consequently plants lose water and cell water, osmotic, and turgor potentials decrease. Inadequate availability of water has profound effects on various plant processes. Plant responses to water stress have been discussed in detail by several authors: e.g., Hsiao (1973), Fisher and Turner (1978), and Hanson and Hitz (1982). In general, plant processes have different time scales in their response to drought (Sinha, 1987). Changes in leaf water potential, turgor pressure, and stomatal resistance occur within seconds or minutes, while cell growth and the degradation of proteins and polysaccharides are effected in hours. Observable effects on leaf expansion, shoot and root growth might take days, but the influence on reproductive biology and grain yield is seen in days or months. Mild water stress decreases cell expansion and thereby growth of leaves, and may slow photosynthesis by feedback inhibition through accumulation of assimilates (Hsiao, 1973). Photosynthesis under greater stress is slowed by stomatal closure and the ratio of photorespiration to net photosynthesis may increase due to the decrease in the CO_2/O_2 ratio within the leaf. Also with an inadequate CO_2 supply photosynthetic cells may become photoinhibited under large solar energy loads. Severe water stress inhibits photosynthesis and causes imbalance between metabolic processes which greatly alters the content of metabolites, and disrupts cellular function (Lawlor, 1987).

Several general patterns of plant moisture stress can be identified in the world (Edmeades *et al.*, 1989). The one relevant to the present investigation is the Mediterranean. In this kind of environment most precipitation falls in winter before the autumn-sown crops reach full ground cover, and moisture deficit rises with temperature in spring. This is the typical pattern of the Mediterranean environments in west Asia, north Africa, southern Europe, Chile, south Africa and western Australia. In these areas, rainfall is highly variable both in amount and distribution, and the stresses are erratic and unpredictable in frequency, severity, and timing. The above-mentioned low mean yields recorded in WANA are the most evident effect of drought, but do not reveal the real dimension of the problem, as they often result from a mixture of relatively good yields and crop failures, both occurring unpredictably (Srivastava, 1987; Austin, 1989).

Austin (1989) discussed the physiology of yield in cereal crops and analysed the effect of drought on the different yield components (number of ears per unit area of land, number of grains per ear and mean weight per grain). In winter cereals typically grown in a Mediterranean-type environment, such as wheat and barley, tillering occurs during early growth when the evapo-transpirative demand is low relative to the water supply. The number of grains per ear is subject to environmental influences, including drought, and it is often the yield component which varies most in response to season-to-season variation in precipitation. Drought during grain filling, which almost invariably occurs in a Mediterranean climate, hastens leaf senescence, reduces the grain filling period and reduces the mean weight of the grains. Winter cereals show development-dependent adaptive responses to adjust their growth patterns to maximise the yield in the presence of a drought which develops slowly (Austin, 1989). Such adaptation to water deficit reduces leaf expansion and tiller growth, and hastens tiller death, resulting in small plants which set few grains. Therefore, the plants exploit the soil water reserves less rapidly, ensuring that some water is available for grain filling.

A crop growing in a Mediterranean climate where water availability is greatest early in the season and progressively decreases may be favoured by early growth and maturity which increases the proportion of transpiration over soil evaporation. From an agronomic standpoint, new technologies are sought for incorporation into the existing farming systems to make maximum use of the moisture available, thus increasing the crop's water use efficiency (WUE), expressed as:

$$\text{WUE} = \text{Yield per unit area} / \text{Water used to produce yield}$$

(Cooper *et al.*, 1987). Changes in crop management, such as applications of fertilizer (especially nitrogen), improved tillage and better weed control, will all increase the amount of water transpired by the crop (Cooper *et al.*, 1987). The adoption of chemicals to control pests and diseases which destroy, or render ineffective, plant parts that contribute to yield will also improve the water use efficiency (Austin, 1989).

Improving yield in stress environments through agronomic practices implies that farmers can adopt these new, and inevitably more expensive, techniques. However, the majority of farmers in west Asia and north Africa are small holders with less than 10 ha of land (Cooper *et al.*, 1987). The small farms are often subsistence oriented: much of their produce is used for home consumption, particularly durum wheat, dairy products and pulses (Cooper *et al.*, 1987). In many instances subsistence farmers face financial constraints which hinder the adoption of new technologies and the only common agronomic practice is an uncultivated fallow (Cooper *et al.*, 1987).

The release during the last thirty years of "high yielding varieties" gave rise to the hope that the adoption of these varieties could improve the competitivity of the farmers operating at lower levels of both inputs and yields. Unfortunately, the so-called "green revolution" often failed when it sought to transfer a substantial piece of well-established, temperate-zone agricultural technology to poor semi-arid conditions in one step (Simmonds, 1979). The weakest part of the operation was that the varieties alone could not improve yields much in the presence of limiting environmental conditions. Therefore appropriate variety-agronomy 'packages' were promoted which contained water control, fertilizers, weed control and disease control as principal elements (Simmonds, 1979). As already noted, these factors are the ones the subsistence farmers could not afford. Moreover, the high frequency of seasons with low yield or crop failures discourages farmers from using high inputs.

Plant breeding could give a major contribution to sustainable improvement of crop production in the less favourable areas. The identification of crop varieties able to tolerate or escape climatic stresses is the most easily transferable technology to farmers in areas affected by such stresses (Ceccarelli, 1987).

1.2.1 *Breeding for dryland conditions*

The physiologist's definition of drought resistance is the plants capacity to escape, survive or endure damage from water stress, while the breeder defines it as the ability of a crop to grow and yield satisfactorily in areas prone to water deficits (Acevedo and Ceccarelli, 1989).

Breeding for drought resistance can have opposing objectives. For certain dryland farmers the major objective may be high yields in the best years, since they contribute the most to long-term yields. For the subsistence farmer, breeding for plant survival in the worst years may be the major goal to ensure some grain production (Richards, 1982). Stability of yield, defined as decreased number of crop failures in time, is a major concern to cereal improvement under dryland conditions (Ceccarelli *et al.*, 1987a; Acevedo and Ceccarelli, 1989). Because of its social and economic implications, this objective must be pursued regardless of short-term correlated responses in yield potential in more favourable conditions (Ceccarelli, 1987).

Two very different approaches have been used in breeding for stable yield in water-limited environments. The first approach, referred to as the traditional, empirical or synthetic approach, relies on grain yield as the selection criterion, as it integrates all the components that determine yield in a stress environment and is, after all, the ultimate goal for the crop. The second, called the analytical or reductionist approach, relies on the different morphological, phenological, physiological, or biochemical traits which contribute to the mechanisms of adaptation to drought, as a way to increase efficiency of selection. The two criteria should be seen as complementary rather than opposing (Richards, 1982; Ceccarelli, 1987; Acevedo and Ceccarelli, 1989). The real issue is not which approach is best but, for the empirical approach, what is the most efficient way to select directly for yield and, for the analytical one, which traits are likely to be the most influential in improving yields and also meet breeders' needs for characters that can be rapidly screened and have high heritabilities.

The most important question in an empirical breeding programme for dry environments is what is the most efficient environment in which to select. Should selection to improve yield in dry areas be conducted in the stress environment or in favourable environments (Richards, 1982; Ceccarelli, 1987)? The arguments which support the latter are the following: i) selection in a favourable environment is more efficient because environmental variance is lower than genetic variance, and ii) high yielding genotypes in favourable environments will retain their superiority when grown in a stress limited environment (a literature review is quoted in Ceccarelli (1987)). In contrast, a number of authors (a comprehensive list is given in Ceccarelli (1987)) have stated the superior efficiency of direct selection under stress conditions. Implicit in the choice of selection strategy is the recognition that plant characteristics associated with maximum yield in optimal conditions are different from those associated with good performance under severe stress conditions. These are mostly related to plant survival mechanisms (Laing and Fischer, 1977; Fischer and Maurer, 1978; Ceccarelli, 1989; Ceccarelli and Grando, 1991).

It has been thoroughly demonstrated by Ceccarelli (1989) that the apparent contradiction between the conclusions of the supporters of the two breeding philosophies mainly lies in the definition of "stress environment". Figure 3 shows the extent to which such a definition may affect the interpretation of genotype x environment interaction and selection strategies. In presence of a cross-over type

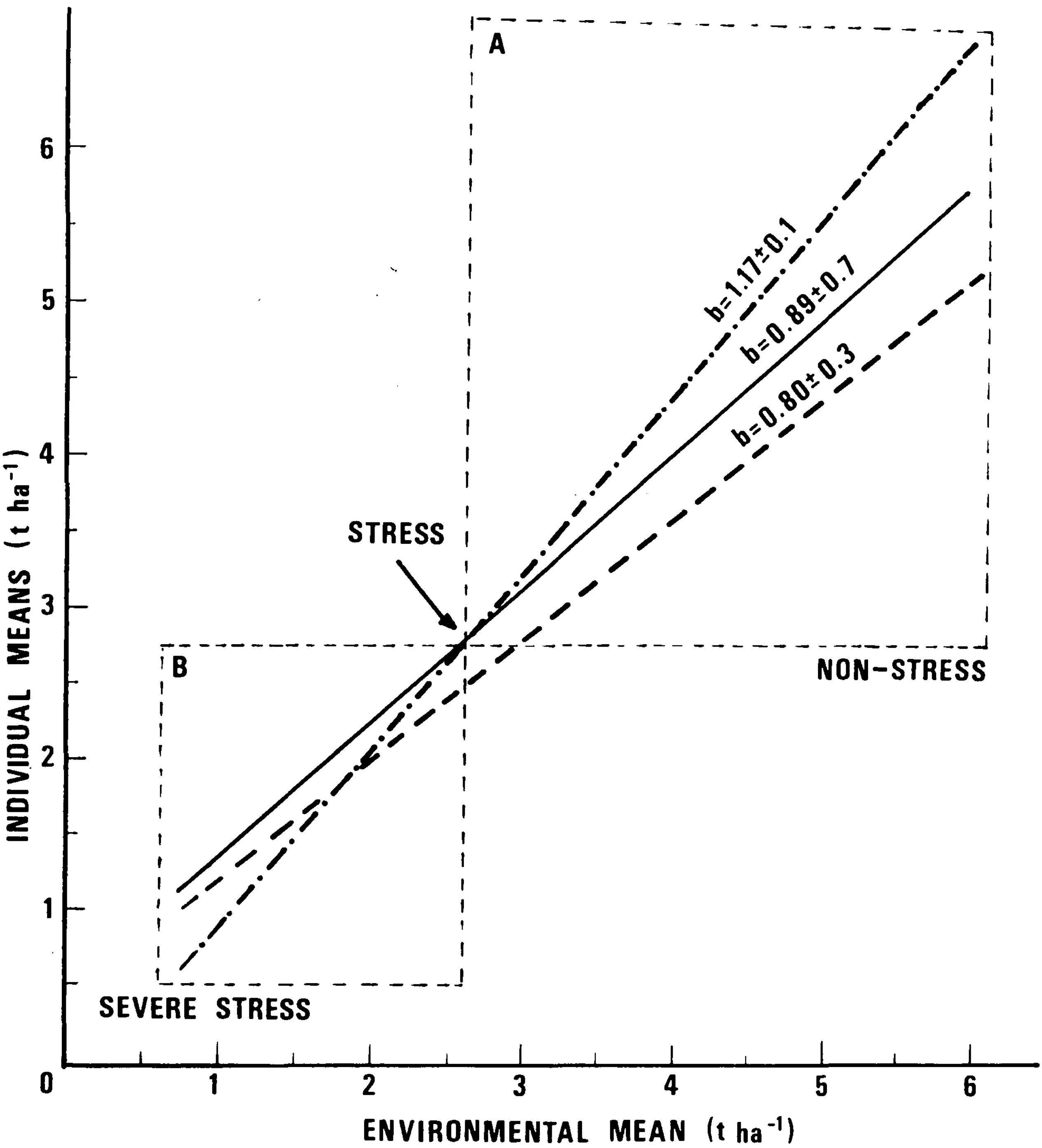


Figure 3. Grain yield (t ha^{-1}) of F_4 bulks of barley from five contrasting environments. Regression lines refer to F_4 bulks selected in a 5-6 t ha^{-1} environment (-·-·-), and in a 1.5-2.0 t ha^{-1} environment (——), and to a landrace (- - - -). From: Ceccarelli (1989).

of interaction (Figure 3) the objectives and the results will change if the range of target environments used in a breeding programme is the one shown in box A or the one in box B. In the former case, with the environment at the left of box A defined as the stress environment, yield improvements under stress conditions can be achieved by selecting high yielding genotypes under optimal conditions. In contrast, if we define as target environment the one in box B, it is evident that: i) the highest yielding genotypes in an optimal environment are generally very poor in a highly stressed environment; and ii) the highest yielding genotypes under severe stress cannot be identified if the breeding material is grown only in a high yielding environment. Considering barley experimental bulks, Ceccarelli (1989) identified at about 2.5 t ha^{-1} the environmental mean yield in which the cross-over occurred. Richards (1982, Figure 2) and Annicchiarico and Pecetti (1988, Figure 4) showed that in durum wheat genotypes the cross-over point may correspond to a lower mean yield of about 1.2 t ha^{-1}. Taking this value to define the highest limit of the 'target environment' within box B in the hypothetical representation of the genotype-environment relationship, most of the durum wheat growing areas in WANA, where mean yields are between 0.5 and 1.1 t ha^{-1} (Srivastava, 1984), should represent an environment for which specific yield improvement is needed. That selection for yield under high yielding conditions is not an efficient criterion to identify superior genotypes under low yielding conditions has been repeatedly shown in Syria for barley (Ceccarelli and Grando, 1991), bread and durum wheat (Ceccarelli *et al.*, 1987a; Pecetti *et al.*, 1992b). These results indicate that selection should be carried out in the environment for which the crop is intended. In particular, selection for dryland areas should be done in dry environments. A drawback to this goal is the reduction in the heritability of yield caused by stress environments. These are usually characterised by larger environmental variance than non-stress environments, increasing the difficulties in relating the phenotype with the genotype. The difficulties become even greater in environments characterised by unpredictable variability in the frequency, timing and severity of climatic stresses.

The difficulties inherent in selecting directly for yield lead to the interest in selecting for traits other than yield in plant breeding programmes for dryland conditions. In this respect, it is essential to understand the physiological and biochemical mechanisms underlying stress resistance, in order to determine which characters could be used in addition to grain yield under drought to increase selection efficiency. By means of this strategy, the desirable integration between the two above-mentioned approaches (the empirical and the analytical) could be attained (Ceccarelli, 1987).

There have been many attempts to classify mechanisms conferring drought resistance in plants. For instance, Turner (1979) listed three types of drought resistance, viz: 1) drought escape: the ability of a plant to complete its lifecycle before serious plant and soil water deficits develop; 2) drought tolerance with high tissue water potentials: the ability of a plant to endure periods without significant water supply while maintaining a high plant water status. This is sometimes referred to as drought avoidance (Levitt, 1972) or dehydration postponement (Kramer, 1980); 3) drought tolerance with low tissue water potentials: the ability of a plant to endure periods without significant water supply and to endure low tissue water potentials, also defined as dehydration tolerance (Kramer, 1980).

The ideal trait to be used as an additional or alternative selection criterion to yield in breeding for stress conditions should satisfy the following requirements: 1) be causally related or genetically linked to yield under stress conditions; 2) exhibit genetic variation; 3) be highly heritable; 4) be easy, inexpensive, and quick to screen (Ceccarelli *et al.*, 1991). An additional requirement is that the trait should not decrease yield in better environments (Richards, 1982). For most traits that appear related to drought resistance the genes involved and their heritabilities are, however, little, if at all, known.

Several lists of putative traits expected to lead to improved yield under drought have been presented. Different aspects of the selection for these characters were examined. For instance, the type of stress, the involved resistance mechanisms, the screening capability, the ease of genetic manipulation, the heritability, the value as selection criterion, the correlated attributes and/or consequential effects, the relationship with the major yield determinant under drought (usable water, water use efficiency, harvest index). An incomplete review includes Turner (1979), Richards (1982), Clarke (1987), Austin (1987), Bidinger and Witcombe (1989), Acevedo and Ceccarelli (1989), Acevedo (1991), Nachit and Ketata (1991), Stockle (1991). Practically any "component" of the plant structure and any phase of the growth cycle can be considered for possible screening, from the cell to the crop canopy and from germination to maturity. At least 50 traits have been tested in studies related to drought resistance. However, in most cases their worth has not been consistently proved and use of these criteria in breeding programmes has been scarce (Richards, 1982). One reason for the limited success may be that the stated conclusions are affected by the low number of genotypes involved, or by the particular type of germplasm used, or by the insufficient number of environments (Ceccarelli *et al.*, 1991). Passioura (1986) identified another reason for the lack of success as the difficulty of integrating a number of mostly short-term processes over the whole growing season. Yield differences under stress conditions are likely to result from a complex of interacting attributes which are not, when taken in isolation, necessarily closely associated with yield under stress. It is therefore likely that, because of the interactions between characters, different genotypes may achieve similar yield through different combinations of traits as suggested by Ceccarelli *et al.* (1991) for barley and Annicchiarico and Pecetti (1993) for durum wheat. Analytical breeding to enhance yield stability in stress environments should consider individual traits as part of an architecture rather than in isolation.

The chances of identifying a superior line increase as the number of genotypes tested increases, particularly in the case of lower selection efficiency (Ceccarelli and Grando, 1991). Adequate yield testing of a large number of entries is very expensive in labour and resources and breeding programmes of large size are generally beyond the possibilities of countries where crop varieties for low yielding conditions are most needed. Any simple, rapid technique that will upgrade the basic germplasm prior to the application of a yield trial will be of a great value to the breeder. Such a technique would be of paramount importance in the selection of parental materials (Townley-Smith and Hurd, 1979). In order to utilize limited resources most efficiently, it is essential that the characteristics desired in a new cultivar be present in at least one of the parental genotypes.

When evaluating a large number of accessions, such as a germplasm collection, for valuable materials for crop improvement under drought, experiments involving replicated plots of suitable size for grain yield assessment can be difficult to perform, due to often limited seed availability and means at disposal. The ICARDA durum wheat collection, comprising about 12000 entries was evaluated for drought resistance at a dry site of northern Syria, allocating single-row plots to individual accessions. With such plot size grain yield could be biased due to intervarietal competition (Jensen and Federer, 1965; Fisher, 1978; Romani *et al.*, 1993), especially when adjacent rows are different in plant height, and particularly in drier conditions. The potential of the tested materials under the given stress was therefore assessed through a visual estimation, based on plant features possibly little affected by the competition. An agronomic score was devised for this evaluation as described by Annicchiarico and Pecetti (1990). Visual scoring has been used for drought resistance in field screening of rice (Chang *et al.*, 1974; Chang and Loresto, 1986). Clarke *et al.* (1991) have adopted a visual agronomic score in a preliminary selection of durum wheat germplasm in a dry growing season and highlighted its efficacy in selecting genotypes that subsequently yielded well in dry environments. The 9-level score adopted in the present evaluation was based on the assumption that good performance under stress would rely on earliness of flowering and maturity (expected to contribute to stress escape) and/or good plant vigour (absence of signs of suffering such as wilting, senescence, stunted growth, etc.) with an apparently good spike fertility (these traits being considered as possible indicators of stress tolerance in its broad sense). That is, the visual evaluation tried to take into consideration the various mechanisms conferring drought resistance. Screening by the visual score was quick and relatively easy to learn. Prior to the actual assessment of individual entries, it was important for the evaluator(s) to walk across the experimental field, trying to associate each score definition with one or possibly more real cases. Bearing in mind (and checking again from time to time) these plots as 'standard' samples of the score helped later to attribute the most appropriate score to each entry. Results from a specific study on this method of evaluation (Annicchiarico and Pecetti, 1990) conducted on standard-size plots (6 rows, 2.5 m long, 0.3 m apart), and recording also grain yield, were very promising. The score proved able both to discriminate materials under evaluation (highly significant variation among accessions was found for the character) and to give a good prediction of grain yield under drought conditions ($r=0.82$ and 0.88, $P<0.01$, at two stress sites). When compared to randomly selected germplasm, the materials selected from the collection according to the score recorded on the single-row plots showed grain yield advantages of 32.8 and 74.3% at two stress sites (234 mm and 193 mm annual rainfall, respectively) in a subsequent season. The score seemed, therefore, suitable in describing drought resistance both in the preliminary evaluation of a large germplasm collection and in the further evaluation of élite germplasm conducive to the selection of parental materials.

1.2.2 *Osmotic adjustment*

Of the many physiological traits advocated to contribute to drought resistance, one of the most discussed is the capability of osmotic adjustment, also known as 'osmoregulation'. Osmotic adjustment has been recognised for a long time as an important mechanism in salinity tolerance. More recently it has been proposed as an important response to water deficit (literature reviews concerning both stresses were provided by Turner (1979) and Al-Dakheel (1991)). Genetic variation for the ability to adjust cellular osmotic potential has been shown to exist within many species of cereals, including wheat, barley, sorghum and rice, and other crops such as pigeon pea, sunflower and *Brassica* species (reviewed by Turner (1979), Morgan (1989) and Al-Dakheel (1991)). The process represents a true tolerance mechanism, involving the active accumulation of solutes in response to a decline in external water potential. This leads to the lowering of the osmotic potential and reduces the outflow of water from the cell, consequently reducing loss of turgor pressure (Morgan, 1989). This maintenance of cell turgor enhances a wide range of turgor-dependent processes (Morgan, 1989, Figure 4.1). Osmotic adjustment may be regarded as one of the primary or causal processes contributing to growth and yield. Turgor pressure maintenance within plant tissue favours cell expansion (Hsiao *et al*, 1976), stomatal opening (Turner *et al.*, 1978, Acevedo and Massardo, 1984) and photosynthesis (Jones and Rawson, 1979). Also maintenance of positive turgor prevents large increases in abscisic acid, thereby maintaining seed set and spike development (Morgan, 1980). It has also been found that wheat genotypes with osmotic adjustment ability have higher tiller survival and kernel number per tiller than other lines (Morgan, 1983). This in turn maintains harvest index (Morgan and Condon, 1986). Genetic improvement in osmotic adjustment has resulted in lines with higher turgor pressures and rates of extension of roots and shoots (Morgan, 1988). Increased osmotic adjustment has proved a way of increasing soil water extraction, so that leaf water potentials are also maintained despite a greater growth of shoots (Morgan and Condon, 1986). In maintaining stomata open for a longer period of time and allowing water extraction and photosynthesis, osmotic adjustment may enhance yield by increasing the transpirational component (T or WU) of the function determining grain yield under limited moisture conditions (Passioura, 1977). Genotypes with high osmotic adjustment had 50% higher WU than non-adjusting genotypes (Morgan and Condon, 1986). Apart from the positive effect on the reproductive organs already mentioned, the positive relationship between enhanced osmotic adjustment and harvest index may also be attributed to a better retranslocation of photosynthate reserves from other parts of the plant to the grain. This may be due to increased efficiency of the translocation system or to an increase in the duration of the grain filling period (Al-Dakheel, 1991). Positive correlations have been found between grain yield under water deficit and turgor maintenance (Morgan, 1983; Morgan and Condon, 1986; Morgan *et al.*, 1986).

The solutes accumulating during osmotic adjustment have not been clearly identified. Potassium, chloride, organic acids, amino acids and, above all, soluble sugars have been implicated in the process (Turner *et al.*, 1978; Turner, 1979; Munns *et al.*, 1979; Al-Dakheel, 1991). Solutes usually accumulate from current photosynthesis and/or from reduction of some sink demand during growth (Begg and Turner, 1976). If osmotic adjustment is achieved by accumulation of organic molecules, then partition of assimilates between growth and osmotic adjustment would become an important factor in determining yield (Sinha, 1987). This could assume even greater significance if water stress occurs at the time of grain development.

Heritability of the trait has not been estimated. The bimodal distribution of the ability of wheat genotypes to osmotically adjust, and the strong segregation of F_4 progenies into two distinct groups with high and low osmotic adjustment, suggest a simple inheritance with a single (recessive) gene involved (Morgan, 1977; Morgan, 1983). Osmotic adjustment genes have been discovered in *Escherichia coli* (Le Rudulier *et al.*, 1984).

Measurements of osmotic adjustment are rather complex and time-consuming (Al-Dakheel, 1991), which limits their practicality for field screening of large numbers of genotypes, as required in breeding programmes (Clarke, 1987). The possibility of screening wheat genotypes for osmotic adjustment during the early phase of growth in a greenhouse has been suggested (Morgan, 1988). This aspect will be examined in the experimental part of the present investigation (section 5).

1.2.3 *Crop simulation*

Systems analysis and simulation have been used by engineers for more that 30 years. Their success has inspired biologists and agronomists to apply similar techniques in their disciplines. A system is a limited part of reality that contains interrelated elements; a model is a simplified representation of a system and simulation may be defined as the "art" of building mathematical models and the study of their properties with reference to those of the systems (de Wit, 1982).

Crop simulation modelling implies the representation of crop performance by mathematical relationships. Its purposes are both a better understanding of the crop and the prediction of the crop's performance in defined but relevant agricultural environments. Two contrasting types of crop model exist, viz., the mechanistic or explanatory model, and the descriptive or empirical model (de Wit, 1982).

The relevant example of the former is the dynamic crop simulation model, based on interconnected physiological and physical relationships which require environmental inputs and are solved numerous times (hourly or daily) throughout the life of the crop in order to calculate crop development, growth and final yield. The empirical model is represented in its simplest form by the regression model, which contains a single function relating crop yield to environmental variables. The potential and the limits of dynamic simulation models as predictive tools were discussed by Fischer (1984). He concluded that crop modelling could provide unique advantages in several situations. Firstly, it is often the only way of obtaining the quick response required, for example, when a new technology such as a new cultivar arises, or when new lands are to be developed. Secondly, modelling seems the easiest way to account for weather stochasticity, which is an essential consideration in management decisions. The alternative is expensive long-term experimentation: the more the practice interacts with the weather, the more experiments are needed. Thirdly, modelling seems suited to the extrapolation of results from experiments, necessarily controlled in nature and restricted in location, to real farm conditions. Modelling allows two other dimensions to be added to agronomic research, those of time and space that are often difficult to encompass adequately using field experimentation. The limits to what can be achieved depend on the sensitivity of the model to biotic factors (Thornton *et al.*, 1991). Any increase in model sensitivity generally results in increased complexity of the model and in increased data demands for running it. On the other hand, insufficient model sensitivity will allow little to be said about biological response to particular input conditions.

Modelling could be more likely to achieve accurate and useful predictions by having regional targets, even though this might occur at the expense of generality and in the face of an incomplete understanding of underlying processes (Fischer, 1984; Thornton *et al.*, 1991). Once confidence has been established that a crop model can produce similar results to those obtained in a particular region, the model can be used to predict crop growth and development in situations where real field data do not exist. Thus a model can be run using a different soil type, or changing sowing date and rate, or simulating different fertiliser and irrigation applications, or modifying tillage practices, or using a different crop species or cultivar, etc. Models can also simulate crop losses caused by diseases and pests (Fischer, 1984) or water use efficiency under limited moisture conditions (Stockle, 1991). Crop modelling can provide a means for a probabilistic assessment of given plant attributes throughout the range of target environments and thus provide a means to assign priorities to traits (Shorter *et al.*, 1991).

The identification of optimal practices for farming in Mediterranean climates is made difficult by the variability of rainfall. Successful cropping requires management techniques that accumulate moisture and minimise soil evaporation and drainage. Seasonal water supply must be matched with cultivar needs as determined by sowing time, crop density, soil fertility, genetic characteristics, etc. The uncertainty in water supply, along with other important weather variables such as radiation frosts and high temperatures during grain filling, creates a "risky" environment for farmers. Because climate, soils, management and plant characteristics all interact to determine crop yield, an integrated approach through dynamic models of crop growth has been proposed to understand crop response to water deficits and to quantify the farmers' risk (Smith and Harris, 1981; Ritchie, 1984; Stapper and Harris, 1989; Harris, 1991). Although risk analysis should include economic factors in addition to production, the comparison of possible alternative situations may provide a simple understanding of decisions to minimise risk.

In areas with highly variable weather patterns the long-term performance of new cultivars is difficult to assess. Evaluation of advanced lines should involve multi-location trials over a number of seasons. Limited sampling over a few years provides only a narrow window of possible climatic environments that cultivars may encounter. If a multi-site, multi-season experiment is not feasible, simulation studies using crop models could be useful to evaluate genotypes. The impact of temporal or spatial climatic variability in the target region on the performance of advanced lines could then be simulated using historical or synthetically generated weather sequences. This would enable repeats of an experiment over many simulated climate years to produce probability distributions of yield or of any other output of interest for each line. Probability distributions could assist in the selection of those lines that were compatible with yield targets and risk requirements for the region (Shorter *et al.*, 1991; Thornton *et al.*, 1991). The characteristics of the best performing and most stable genotype(s) in the long-run could also permit the identification of the most suitable ideotype(s) for the target region.

1.3 *Salinity*

It seems appropriate to consider together in the present study the effects of both drought and salinity on plant growth and the possible means of screening durum wheat germplasm against such effects. Salinity and drought are related phenomena and represent two of the most important environmental stresses influencing the productivity of agricultural systems, particularly in the arid and semi-arid regions. Both are natural phenomena, but their impact and severity are exacerbated by the activities of Man. The underlying assumption that the processes limiting the growth of plants affected by drought or by salinity are often similar brings together research efforts on the two stresses. Meetings have been organised in which physiologists dealing with drought or with salinity or with both have commonly debated the two maladies: e.g., the Meeting held in Australia in 1986 (Turner and Passioura, 1986) and the one in Spain in 1987 (Acevedo *et al.*, 1991). The similarity between the two stresses lies in the fact that to some extent there is similarity in the water relations of plants affected by drought or by salinity. After all, both substantially lower the water potential in the soil and thence in the plant, causing poor growth (Turner and Passioura, 1986). It has already been mentioned that osmotic adjustment has been observed as a resistance mechanism against both stresses. Peculiar effects on plant growth caused by salinity do exist nonetheless, and will be discussed later.

Salinity is described as "the occurrence of various salts in soil or water in concentrations that may interfere with the growth of plants" (Jana, 1991). Such interference is due to the physical, chemical, and biological properties that a high concentration of electrolytes determines in the soil, resulting in low fertility and limited agricultural value (Szabolcs, 1974). Salinity constitutes an important constraint on agricultural productivity over large areas of both irrigated and rainfed areas in the arid and semi-arid regions (Szabolcs, 1974; Mashali, 1989; Abo El-Enein, 1991). Salinity of soil and water is caused by the presence of soluble salts originating from deteriorating and dissolving rocks and concentrated by evaporation and plant transpiration. In arid and semi-arid environments especially, the scarcity of water and the hot, dry climates frequently cause salinity concentrations that limit or prevent crop production.

In the arid and semi-arid regions, the 'saline soils' predominate, developing mainly under the influence of sodium, chloride and sulphate. Other types of salt-affected soils which occur in these environments are the 'alkali soils', in which CO_3^{2-} and HCO_3^- are the predominant anions, the pH is greater than 8.5, and the EC_e is lower than 4.0 dS m^{-1}, and the 'gypsiferous soils', affected by substantial amounts of soluble calcium salts (Szabolcs, 1974). For west Asia and north Africa, the following data are available (Szabolcs, 1974) on the occurrence of salt-affected soils: >3 million (M) ha in Algeria , >7 M ha in Egypt, ca. 2.5 M ha in Libya, >1 M ha in Morocco, ca. 1 M ha in Tunisia, >27 M ha in Iran, >6.5 M ha in Iraq,

>0.5 M ha in Syria, 2.5 M ha in Turkey. It should be noted that Mediterranean countries of Europe such as Greece, Italy, Portugal and Spain also have considerable areas of salt-affected soils, reaching 0.45 M ha in Italy and 0.84 M ha in Spain (Mashali, 1989).

High salt levels, particularly of sodium, contribute to crusting of the soil, which makes seedling emergence difficult. Incrustations and compactness due to colloid deflocculation limit water infiltration and permeability, reducing efficient drainage and salt leaching. As a result, salt content increases and the soil is saturated, with negative effects on aeration, root penetration and nutrient availability (Shannon, 1984; Mashali, 1989).

Beside these indirect adverse effects of salinity, there are also negative influences of the salt which directly hinder plant life. In the short-term, leaves grow more slowly after exposure to salinity. The response is very rapid, is usually proportional to the osmotic potential of the external solution, and is rapidly reversible (reviewed by Munns and Termaat (1986)). These authors thoroughly investigated the phenomenon in non-halophytes, assessing whether it is caused by a water deficit (osmotic effect) or a specific salt toxicity (ionic effect) in the shoots or in the roots. Their conclusion was that the cause of reduced growth in the short-term is probably a water deficit at the roots, despite the fact that root growth is usually less reduced than shoot growth. They suggested that a message is likely to be transmitted from the roots to the shoots, presumably in the xylem, which regulates metabolic processes in the expanding leaves. The message is possibly the concentration of a hormone or growth regulator. Some compounds (cytokinins, abscisic acid, gibberellic acid, and ethylene) have been suggested as possible regulators, all having in common synthesis in the roots and a rate of synthesis which changes in water-stressed plants (the literature has been reviewed by Munns and Termaat (1986)). Of the possible metabolic processes that could be limiting growth of the shoots, nitrogen supply (reviewed by Munns and Termaat

(1986)) and supply of metabolic energy (Shannon, 1984) might be involved.

A second effect of salinity is usually apparent in the long-term in non-halophytes. It is the result of salt toxicity resulting from the gradual buildup of high salt concentrations in the leaves. In wheat, salt toxicity is particularly apparent following anthesis and is characterised by early senescence and failure of seed set or grain filling (Wyn Jones and Gorham, 1991). Munns and Termaat (1986) concluded that there are specific, toxic effects of Na^+ or Cl^- in the leaves, on top of any osmotic effect of external NaCl on the roots. In non-halophytes, fully expanded leaves are adversely affected long before the young leaves, simply because salt concentrations at a given time are always highest in older leaves (Greenway and Munns, 1980). The oldest leaves die long before young leaves are affected. The higher salt concentration in the older leaves of non-halophytes may result entirely from a product of time by transpiration rate (Greenway and Munns, 1980), or, at least partly, from an exclusion of specific ions from the xylem vessels supplying the younger leaves (Yeo and Flowers, 1982).

The ion relations and compartmentation of leaves of plants growing under saline conditions have been reviewed by Greenway and Munns (1980), Gorham *et al.* (1985a), and by Flowers and Yeo (1986). In contrast to the halophytes (plants that have been naturally selected to grow in saline environments), the monocotyledonous glycophytes, such as the cereals, have a continuous increase with time of Na^+ and Cl^- concentrations in the shoots (Yeo and Flowers, 1982) which exceeds the quantity of ions necessary for osmotic adjustment. A key strategy for a tolerance at the cellular level is therefore a synchronization of ion compartmentation by the leaf cells with a high rate of ion transport to the shoots. It is assumed that a number of species are capable of an efficient ion compartmentation, i.e., accumulation in the vacuole (Greenway and Munns, 1980). In these plants, under saline conditions the large quantities of salts (mainly, but not exclusively, NaCl) that are transported to the leaves are accumulated in the vacuole. The concentration of inorganic ions in the cytoplasm is kept to lower values than that in the vacuole. At the plasmalemma there is a selective uptake of K^+, and an exchange of K^+ for Na^+ occurs in the cytoplasm. At the same time, there exists a selective export of Na^+ across the tonoplast to the vacuole and selective exchange of Na^+ for K^+ in the vacuole (Gorham, 1992). The maintenance of osmotic equilibrium across the tonoplast requires the accumulation in the cytoplasm of non-toxic organic solutes (usually referred to as 'compatible solutes') the nature of which varies among taxonomic groups (Gorham *et al.*, 1985a, Table 1). In the cereal crops an effective vacuolar compartmentation does not seem present, with the possible exceptions of rice (in some cases, as quoted by Greenway and Munns (1980)) and barley, which results the most tolerant cereal despite the high leaf Na concentration observed (Gorham *et al.*, 1990a). However, in this latter species other mechanisms such as selective partition of Na into older leaves and K into growing tissues, or redistribution of these two ions in the phloem are being investigated (reviewed by Gorham *et al.* (1990a)). When the vacuolar compartmentation of inorganic ions is not present, once supplied to the leaf, the fate of these ions is to be accumulated within the plasma membrane (in the symplast), remain in the apoplast or be re-exported *via* the phloem. The latter option is certainly very limited in cereals (reviewed by Flowers and Yeo (1986)). Several grass species present salt glands which are an effective method of controlling the salt content of leaves (Gorham, 1992). None of the cereals, nor their wild relatives possess, however, salt glands. The excess of supply relative to the demand leads to either excessive apoplastic or excessive symplastic ion concentrations. The small volume of the apoplast (e.g., in bread wheat it is 3% of the leaf mesophyll volume (Flowers and Yeo, 1986)) causes faster ion accumulation in the apoplast than in the symplast. The excessive accumulation of ions in the apoplast results in withdrawal of water from the cytoplasm of the neighbouring cells, causing loss of turgor, cellular desiccation and ultimately death (Flowers and Yeo, 1986). If excessive symplastic concentrations occur, ion toxicity interferes with metabolism causing death. The fact that too many old leaves die limits productivity in the long-term. If the rate that old leaves die becomes faster than the rate that new leaves grow, the photosynthetic leaf area will decrease (whether or not the photosynthetic rate is reduced). Eventually, the living leaf area cannot produce enough carbohydrates to sustain the growing parts and the root system: leaf expansion ceases and, shortly after, the plant dies (Munns and Termaat, 1986).

Because salt stress is difficult to separate from several other physical and nutritional stresses, the term "salt stress" is used to mean all salinity-related stresses that cause reduced productivity through partial or complete inhibition of germination, emergence and growth of a crop plant (Jana, 1991).

The best long-term solutions to minimise the extent and spread of saline soils are to provide adequate reclamation, drainage and water control. Unfortunately, solutions that are long-term are also usually expensive. Increasing costs for water and energy reinforce the need for alternative strategies. One such strategy is the genetic improvement of crop tolerance to salinity. An enhanced adaptation to salt-affected soils can extend the area available for cereal production, especially in rainfed areas, and increase yields in areas which suffer from marginal problems of salinity and/or alkalinity. Improvement in salt resistance would also "buy time" in which proper drainage and better management practices could be implemented on less favourable soils (Gorham and Wyn Jones, 1990a). Any improvement in the response to salinity, even small percentage gains in production, are likely to be very valuable in the worst environments.

1.3.1 *Breeding for salinity resistance*

Resistance to salt is a complex phenomenon which involves interactively several different physiological, biochemical, and developmental traits. Growth under saline conditions could be improved if: i) the rate of leaf expansion increased; ii) the maximum ion concentration tolerated by the leaf increased; iii) the rate of leaf ion uptake decreased; or iv) the photosynthetic efficiency of the leaf increased (Munns and Termaat, 1986). The rate of leaf area expansion is governed by the response to low water potential in the soil communicated by the roots to the shoots (Munns and Termaat, 1986). Understanding of these processes might enable the improvement of leaf expansion in saline soils. Cellular tolerance to high NaCl concentrations could be increased by a rapid removal of salt from the apoplast, coupled with an intracellular compartmentation which places the toxic ions in the vacuole and non-toxic osmotica in the cytoplasm. A decrease in the rate of salt accumulation in the shoots will depend mainly on the ability of the roots to exclude salt from the transpiration stream. Any factor which reduces the amount of transpired water per unit of carbon fixed (such as high water use efficiency) would also reduce the salt concentration in the leaves and so prolong their effective life and photosynthetic activity (Munns and Termaat, 1986).

Some of the traits involved in salt resistance (defined by Levitt (1972) as a combination of tolerance and avoidance strategies) are obvious and relatively easy to measure (e.g., salt exclusion from the shoots). Other characters, such as the control of apoplastic salt concentrations in leaves and the compartmentation of solutes within cells, are cryptic and, therefore, difficult to determine in the laboratory and at present impossible to use to screen for salt resistance. Given the cryptic nature of many of these traits, it has been suggested (Yeo and Flowers, 1986) that breeding for salt resistance will be more efficient if a 'pyramiding' approach is adopted, i.e., the integration of useful, individual physiological, biochemical, or developmental traits identified by different screening methods.

Ideally, a breeder would like to find out what makes a glycophyte, such as wheat or barley, salt tolerant (in the broadest sense of the term), identify the gene(s) responsible for these traits, then undertake a breeding programme to transfer the gene(s) into an agronomically desirable background.

Progress has been made in recent years on two related but not identical characters affecting salt resistance in the *Triticeae*: salt exclusion, or tight control of salt influx, and the enhanced K/Na discrimination character. The former character is a feature of some perennial species, particularly of the genera *Leymus* and *Thinopyrum* (Gorham, 1992). It is also found in full or partial amphiploids between these wheatgrasses and wheat (Gorham *et al.*, 1986; Forster *et al.*, 1987; Hollington *et al.*, 1992). One of the main objectives of these investigations was indeed the identification of possible sources of salt resistance which could be used to improve the tolerance of wheat through wide hybridization. These species are able to limit the accumulation of Na and Cl in the leaves to a level which does not exceed that required for osmotic adjustment (Gorham *et al.*, 1985; Gorham *et al.*, 1986). Experimental evidence (Forster *et al.*, 1988) shows that the chromosome 5J ($5E^j$) of *Thinopyrum bessarabicum* (Sav. et Ray.) Löve carries gene(s) for Na exclusion from the leaves and roots. Mahmood and Quarrie (1993) have recently reached the same conclusion. Restriction of salt accumulation is evident particularly at higher salinity (>200 mol m^{-3} NaCl).

The enhanced K/Na discrimination character was first observed in a study of ion accumulation in the ancestors of bread wheat. Hexaploid wheat and the D-genome ancestor, *Aegilops squarrosa*, accumulated less Na and retained more K than tetraploid wheat (Wyn Jones *et al.*, 1984) when grown at 100 mol m^{-3} NaCl. Synthetic hexaploid wheats, in which the D genome of *Ae. squarrosa* was combined with B and A genomes of tetraploid wheat, also showed enhanced K/Na discrimination (Shah *et al.*, 1987). Analysis of aneuploid and substitution lines of tetraploid and hexaploid wheats revealed that the character was located on the long arm of chromosome 4D (Gorham *et al.*, 1987). The main physiological characteristics of the trait can be summarized as follows (Gorham, 1993): i) it controls K and Na transport from roots to shoots, possibly at the point of xylem loading; ii) it has no major effects on root cation concentrations; iii) it has no major effects on anion concentrations in the root or the shoot; iv) it operates at all salinities, i.e., it is constitutive; v) it is most obvious at low salinities where other mechanisms are less important; and vi) it enhances a discrimination which is present in all plants.

The enhanced K/Na discrimination character has also been revealed in A-genome diploid wheats, probably on chromosome 4A (Gorham, 1990; Gorham *et al.*, 1991) and in GGAA-genome tetraploid wheats (Gorham, 1990), but not in BBAA-genome tetraploid wheats, both wild (*T. dicoccoides* (Körn) Schweinf.) and cultivated (*durum* group) (Gorham, 1990; Gorham *et al.*, 1991). Loss of expression may be associated with the considerable chromosomal rearrangements involving chromosome 4A which have occurred during the evolution of most polyploid wheats (reviewed in Gorham *et al.* (1991)). The character does not occur in barley which is one of the most salt-tolerant of the annual *Triticeae* (Gorham *et al.*, 1990b).

The enhanced K/Na discrimination trait identified in the D-genome should help to improve the salt and alkali tolerance of tetraploid wheat if it can be incorporated into a tetraploid background without the detrimental effects of other genes located on chromosome 4D. Attempts to measure the salt tolerance of D-genome substitution lines in tetraploid wheat were frustrated by the poor performance of the aneuploid lines compared to the euploid controls (Gorham *et al.*, 1990a). To overcome this problem, a number of recombinant lines have been produced, based on the tetraploid wheat variety 'S. Cappelli'. These lines contain small fragments of the long arm of chromosome 4D from the hexaploid variety 'Chinese Spring'. Grown in 50 mol m^{-3} NaCl or with ^{22}Na in low-salt solutions, these lines behaved in two distinct ways: one group was similar to the hexaploid wheat and appeared to have the enhanced K/Na discrimination trait; the second group was similar to the tetraploid parent, without this character (Gorham, 1993). The trait is controlled by a single gene locus, designated as *Kna-1* (Dvorák and Gorham, 1992). The effective worth for salt tolerance of the recombinant lines bearing the portion of the chromosome 4D where the locus is located is currently under investigation.

There is experimental evidence to affirm that enhanced K/Na discrimination is not the only factor affecting salt resistance in the *Triticeae* (Gorham, 1993). As already mentioned, in spite of lacking this trait barley is recognised as the most tolerant of the cultivated winter cereals (literature cited in Gorham *et al.* (1990b)). Also *T. dicoccoides* lacks the character; however, wide variation between populations of this species has been found in ^{22}Na uptake which also corresponded to variation in salt tolerance (Nevo *et al.*, 1992). The variation reported is probably the result of differences between populations in other aspect(s) of sodium transport than enhanced K/Na discrimination.

Several studies have demonstrated that tetraploid wheats are the least tolerant to the stress (reviewed by Gorham *et al.* (1990a)). On the other hand, durum wheat is the most important food crop in west Asia and north Africa and the need for improving the crop, and widening its adaptation to a broad range of agro-climatic conditions that prevail in the region cannot be overemphasized. Breeding could perhaps improve the resistance of durum wheat provided sufficient variation among genotypes is found. Because mechanisms of salt resistance in tetraploid wheat are unknown, it is necessary to develop broad-based breeding populations (germplasm pools) to identify genotypes that could be later used as gene sources. One source of variation that has not been fully exploited is that within 'genetic resources', i.e., old cultivars, landraces and wild evolutionary relatives. Variation does exists within these genetic resources for salt resistance. This has been shown for *T. dicoccoides* by the studies of Nevo *et al.* (1992, 1993). Mithal and Koppar (1990) reported 14 landraces of *T. durum* and one of *T. dicoccum*, collected in several states of India, as tolerant to salinity when screened at the Central Soil Salinity Research Institute, Karnal. At least, screening germplasm collections could allow the identification of suitable genotypes which would prove relatively less susceptible than others, to be used as possible recipients for the introgression of identified resistance mechanisms, such as those previously described.

1.4 *Genetic resources*

Successful plant breeding tends to narrow the genetic base of a crop in rough proportion to its success (Simmonds, 1979). The adoption of modern, genetically uniform varieties has introduced a greater risk of vulnerability to pests and diseases in more favourable environments (Simmonds, 1979), and has resulted in a reduction of performance stability under unfavourable conditions (Porceddu *et al.*, 1988). As already mentioned about the effect of the 'green revolution' on low-input farming systems (see section 1.2.1), in many instances the impact of "advanced" plant breeding on agricultural production of these systems has been negligible (Damania, 1991, Figure 1). Experimental evidence (e.g., Ceccarelli and Grando, 1989, 1991) suggests that one possible reason for this lack of success is the large genotype-environment interaction, resulting from the fact that a considerable amount of plant breeding work for less favourable conditions has been based on direct introduction of cultivars bred elsewhere and/or for better conditions. It has been suggested (section 1.2.1) that a higher efficiency of selection can be achieved by separate breeding programmes for different environments. A second key to successful breeding for low-yielding conditions is the use of adapted germplasm. Usually the most adapted germplasm is the one that has been able to coevolve with the environment in which it grows in relatively undisturbed niches. That is the case of the so-called 'non-conventional' germplasm, which includes for wheat: landraces, primitive cultivated species, wild progenitors and other wild relatives (Damania, 1991), the whole of which is usually referred to as 'genetic resources' (Frankel and Hawkes, 1975). In the last 15 years or so, an overwhelming literature has been produced on the utilization in crop improvement of such genetic resources in many species. Certainly incomplete reviews are reported by Chang (1985), Porceddu *et al.* (1988), Damania (1990) and Damania (1991). For obvious reasons - not least the fact that they are cultivated populations of the same crop species one is trying to improve and, therefore, are readily crossable with any other genotype - the landraces have been the most used genetic resources by breeders. Although in wheat the crossability between wild and cultivated species has been substantially improved by the adoption of cytogenetic strategies of intervention in the regulation of meiotic pairing to induce alien chromosomes to pair with their wheat homoeologues (reviewed by Ceoloni (1987)), there remain some constraints to the exploitation of wild species in wheat breeding. Firstly, collections of wild species in the past have been fragmentary and scanty and materials presently available are not representative; secondly, work on wild forms has primarily concentrated on evolutionary and taxonomic studies; and thirdly, variability within populations of wild species has not been looked at in adequate detail (Srivastava *et al.*, 1988).

Natural plant populations and populations of landraces are genetically variable (see, for instance, Nevo *et al.* (1992) and the literature reviewed there; Brown (1978); Porceddu and Scarascia Mugnozza (1983); Ceccarelli *et al.* (1987b)). Quantitative variation conferred by the synergistic action of large number of genes of individually small effects permits sensitive responses to even minor environmental influences. In the landraces this has permitted the evolution of numerous locally adapted populations. Landraces peculiarly also possess adaptive complexes associated with the special conditions of cultivation, which may be of special interest to plant breeders. The release of adaptively responsive variation is attained along with the maintenance of a certain level of heterozigosity sufficient to ensure that reserves of variability continue to exist. Characteristically high levels of heterozigosity have been found to occur in natural populations, even in self-pollinating species (reviewed by Bennett (1970)). Heterozygous individuals have phenotypic plasticity which is of great adaptive significance in environments characterised by marked, short-term climatic fluctuations, as it ensures a quick, dynamic response to the changes in the environment. These genotypes act as a buffer for the population and contribute to maintaining the stability of the population. As Ceccarelli *et al.* (1991) stated: "The stability of the individuals is sacrificed to maximise the stability of the population.".

Given the localized origin of landraces and wild populations, even a relatively small geographic distance can harbour substantial variation. This has been observed in *T. dicoccoides* from Israel (Nevo *et al.*, 1984), Jordan (Jaradat *et al.*, 1988) and Turkey (Nevo *et al.*, 1988), in *Aegilops* spp. from Syria (Rifaie *et al.*, 1981); in durum wheat landraces from Yemen (Damania and Porceddu, 1983), Israel (Poiarkova and Blum, 1983), east Aegean islands (Biesantz *et al.*, 1990), Sicily (Boggini *et al.*, 1990), Iran (Attary, 1990), Jordan (Jaradat, 1991a, 1991b), Syria (Elings, 1991), Portugal (Pecetti, 1992) and Morocco (Pecetti and Nachit, 1993). Whenever the reason for such variation was looked for, it was always found that it depended on the agro-ecological (mainly climatic) conditions of the sites where the populations grew (Nevo *et al.*, 1988; Nevo *et al.*, 1992; Jaradat, 1991b; Elings, 1991; Pecetti and Nachit, 1993). Variation was also found at a higher, and somewhat arbitrary, geographic level, such as between countries (Jain *et al.*, 1975; Porceddu, 1976; Pecetti and Annicchiarico, 1991; Pecetti *et al.*, 1992a; Pecetti *et al.*, 1992c; Pecetti *et al.*, 1993). Also in this case the environment played a major role in creating the overall variation for some important adaptive traits (Pecetti *et al.*, 1992a). The genetic resources represent therefore a reservoir of variability at various stages, from intra-population to inter-populations, to inter-countries. The importance of such reservoir lies in the fact that the success of breeding depends on the availability of sufficient genetic variability for any character of concern (Richards, 1982).

In developing countries, landraces are still the backbone of agricultural systems, mainly in unfavourable environments. In most countries of the ICARDA region, indigenous landraces do represent the largest portion of cultivated durum wheat varieties (Table 3). However, there exists a great risk of genetic erosion which is taking place at an alarming rate in the principal centres of diversity of the crop, such as Ethiopia and the Mediterranean basin (Perrino and Porceddu, 1990). Developing countries, where improving crop production under low-yielding conditions is important, should consider their landraces as the basic breeding material in their programmes. The existing variability in such populations may be used either directly through simple breeding methods such as mass selection or pure-line selection to improve the adapted germplasm (Ceccarelli *et al.*, 1991), or indirectly utilizing the best selections (for specific traits) from landraces as parents in crosses with either other selections from landraces or introduced germplasm. An alternative long-term and sustainable improvement of yield stability in low-input environments has been proposed (Ceccarelli *et al.*, 1991) and is based on populational buffering as achievable with mixtures of genotypes representing different, but equally successful, combinations of traits, as occurs in landraces.

As regards durum wheat improvement for drought tolerance, great variation has been found in collections of genetic resources screened either directly for their response under stress conditions or for characters which may contribute to good

Table 3. Percentage distribution of durum wheat varieties in the countries of the ICARDA region. From: Srivastava and Damania (1989).

Country	Indigenous varieties or landraces(%)	Improved cultivars (%)	New high yielding varieties (%)
Afghanistan	90	0	10
Algeria	85	0	15
Cyprus	0	90	10
Ethiopia	100	0	0
Iran	100	0	0
Iraq	25	65	20
Jordan	20	80	0
Lebanon	30	65	5
Libya	0	55	45
Morocco	50	50	0
Saudi Arabia	100	0	0
Syria	64	29	7
Tunisia	0	65	35
Turkey	10	40	50
Pakistan	88	0	12

and stable performance. Promising genotypes have been identified in the landrace collections evaluated by Pecetti and Annicchiarico (1991), Clarke *et al.*, (1991), Annicchiarico and Pecetti (1993), Pecetti and Annicchiarico (1993). In different dry Mediterranean regions, breeding programmes seek to combine the favourable adaptive traits of landraces with the high yield potential of modern genotypes: e.g., Duwayri *et al.* (1987) in Jordan, Boggini *et al.* (1990) in Sicily, Daaloul *et al.* (1990) in Tunisia. Given the wide year-to-year precipitation fluctuations typical of these regions, this strategy aims at producing varieties with a high level of yield stability to prevent crop failures in the unfavourable seasons and obtain satisfactory yields in the favourable seasons. This breeding approach is also adopted at ICARDA (Srivastava, 1987), where successful varieties from crosses between landraces and high-yielding cultivars are available: 'Om Rabi', obtained crossing 'Jori 69' with 'Haurani', and 'Kabir', obtained crossing 'Flamingo' with 'S. Cappelli'. The case of 'S. Cappelli' is emblematic of the importance that landraces can assume in plant breeding. This 80-year-old Italian cultivar was obtained through mass selection from a population of the north African landrace 'Jennah Khetifa' and soon became the leading variety in Italy where it was sown on an area >0.7 M ha just after the second world war. In 1985 it still occupied 92000 ha. 'S. Cappelli' was widely and successfully adopted as a parent in all breeding programmes in Italy, so that nowadays most cultivated durum wheat varieties have it in either or both parental genealogies (Boggini *et al.*, 1992). The outstanding adaptation of 'S. Cappelli' to dry Mediterranean conditions made it successful not only in its country of selection but wherever the conditions were similar, and its cultivation spread. In Syria it has been officially reclassified as a local variety. In a collection of durum wheat germplasm, outstanding specimens of 'S. Cappelli' (or of its crosses with other landraces, such as 'Capeiti', obtained by crossing it with the middle east landrace 'Eiti') were identified within accessions from Greece, Jordan and Chile (Pecetti and Annicchiarico, 1991). Another case of an exotic, drought tolerant landrace which has been adopted far removed from its origin and is used in breeding programmes is 'Pelissier' that was introduced into north America from Algeria in 1896 and has become very common in the dry Canadian region of Saskatchewan (Clarke, 1987).

The value of landraces has usually been assessed only on an adaptation basis. However, they may also have a great potentiality to improve qualitative traits of great importance in traditionally durum-wheat-growing areas (Blum *et al.*, 1987; Boggini *et al.*, 1990; Pecetti *et al.*, 1992c; Pecetti and Annicchiarico, 1993).

Primitive and wild wheats are also being evaluated for their adaptation to dryland conditions, and utilized to improve durum wheat through wide crossing (Nachit, 1991). Interesting variation has been reported as regards *T. dicoccoides* (ICARDA, 1986; Jaradat and Humeid, 1990), *T. dicoccum* (Hakim *et al.*, 1992), *T. polonicum* (H. Mekbib, pers. comm.) and *Aegilops* spp. (Damania and Pecetti, 1990). Promising results were obtained by Tahir and Pashayani (1990) for cold tolerance, yellow rust resistance and protein content by crossing durum wheat (either landraces or improved germplasm) with *T. dicoccoides*, *Aegilops kotschyi* Boiss. or *Triticum zhukovski* Men. et Er. Variation for physiological mechanisms of drought resistance (maintenance of high leaf water potential at decreasing soil water content, maintenance of high stomatal aperture, high CO_2 fixation rate and high relative water content at decreasing leaf water potential) was found by Shimshi *et al.* (1982) between wheat-related wild species, with *Ae. kotschyi* ranking best followed by *Ae. longissima* Schweinf. et Muschl. Some released ICARDA durum wheat varieties or breeding lines include primitive wheats in their pedigrees, such as *T. polonicum* in 'Sebou' and *T. dicoccum* in 'Sahl', 'Hagla' and 'Jabbul'.

The importance and the potential of the wild wheat species for the improvement of salt resistance in durum wheat has already been mentioned (section

1.3) with special reference to the work carried out by Dr. J. Gorham and his colleagues in Bangor. Sayed (1985) showed a variable response (measured in terms of plant survival both at the seedling stage and at maturity) in diploid and tetraploid wheats to high levels of salinity. *T. dicoccum* seemed to have a high level of salt tolerance. The same study (Sayed, 1985) also presented interestingly high levels of tolerance in a durum wheat collection both at the seedling stage and at maturity. USA and Egypt were the sources of the greatest proportion of tolerant lines. Sayed (1985) concluded that the optimum strategy for future work on salt tolerance should concentrate on screening entries in collections from arid and semi-arid regions. As already mentioned, salt tolerance has also been detected in Indian durum wheat landraces (Mithal and Koppar, 1990).

The results previously discussed indicate that genetic resources, particularly landraces, are a source of readily available genetic diversity which can be used as a short-term strategy in breeding for tolerance to abiotic stresses (their possible use in breeding for tolerance to biotic stresses, although existing and very valuable, is out of the scope of the present study).

All the materials utilized in the experiments described below represented samples from the available collections of durum wheat genetic resources at ICARDA.

2 *Field assessment of durum wheat performance in northern Syria: Breda 1988-90*

2.1 *Introduction*

It has been previously discussed (see section 1.2.1) how critical the choice of the optimal selection environment is in plant breeding programmes (i.e., the environment which maximises the response for the target area). This is particularly important when yield of the target area is low due to climatic stresses and/or low inputs (Ceccarelli and Grando, 1991).

The Cereal Improvement Programme of ICARDA has used since the late 1970's an experimental station near the village of Breda, Aleppo, as its test site for drought tolerance assessment. In this section some features of the location which make it suitable and useful for this purpose are presented.

Breda is situated 40 km due south from the city of Aleppo (north-west Syria) at 35°56' latitude north, 37°10' longitude east and at an elevation of 300 m asl. It lies in a vast plain stretching south-east into the Syrian steppe between two ranges of hills about 500-700 m asl high (ICARDA, 1991). In north-west Syria, annual rainfall decreases rapidly on an eastward gradient and, to a lesser extent, towards the south (Figure 4). In the wetter western and north-western part of the area, wheat-based farming systems dominate, whereas moving towards the south-east the drier part is occupied by barley-livestock systems. Breda is situated between the 250 mm and 300 mm isohyets (Figure 4), roughly on the more favourable edge of the barley-growing area. Although at the margin of the durum wheat belt, the locality is representative of a very important agro-ecological zone for

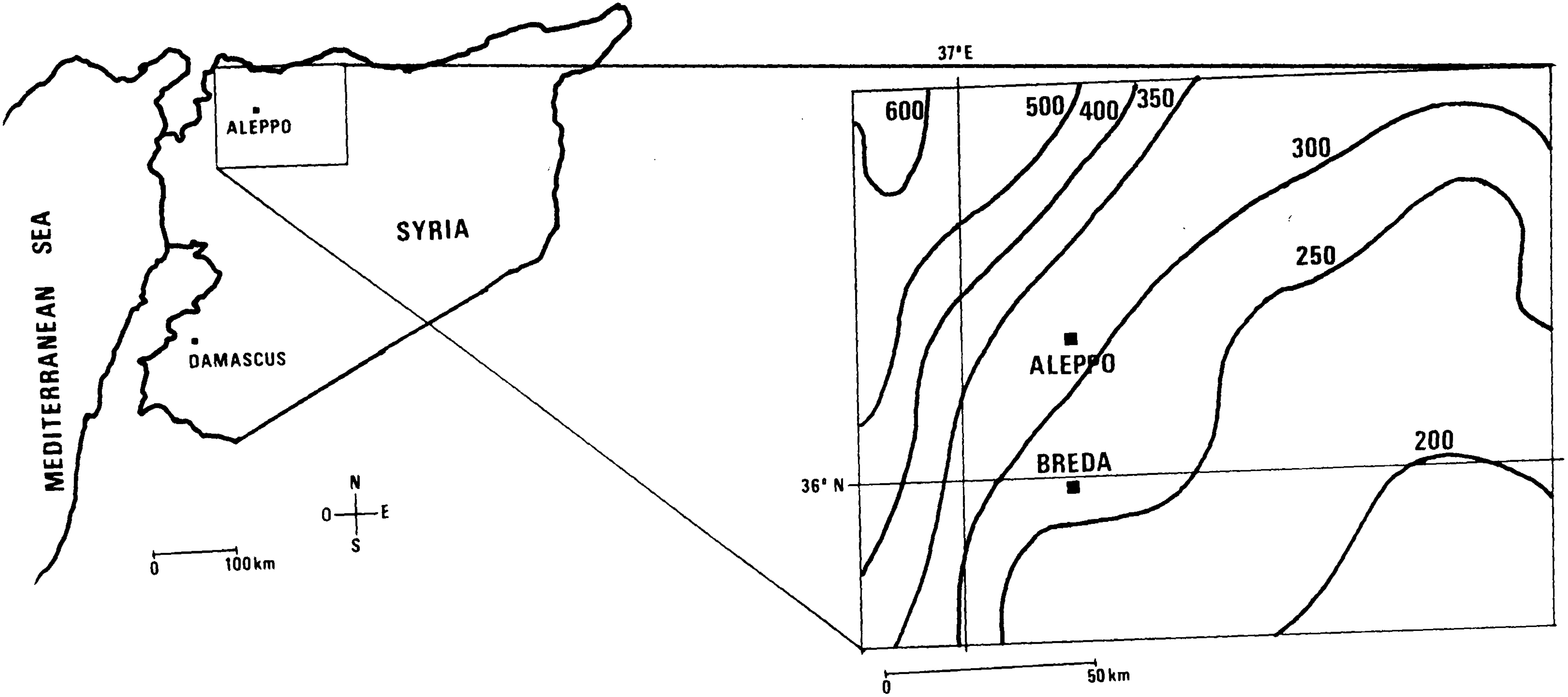


Figure 4. Location of Breda experimental station in northern Syria with approximate rainfall isohyets (mm). From: Dennett *et al.* (1984).

durum wheat in west Asia and north Africa (WANA), viz., the one characterised by low rainfall (<350 mm) with low winter temperature. This zone covers approximately 40% (3.5 million ha) of the total durum wheat area in WANA. The major production constraints are drought and cold during the vegetative phase, and terminal drought/heat stress during the grain filling period. Yearly weather variations are very large, and crop reductions and failures due to climatic fluctuations occur often. Stem sawflies and suni bugs frequently cause damage while yellow rust and common bunt are major diseases occurring in relatively wetter seasons. This kind of environment is present in the continental areas of Morocco, Algeria, Syria, Turkey, Iraq and Iran (Nachit, 1988).

Breda corresponds very well to this picture, both climatically and in terms of yield response. The average annual rainfall in the period 1980-1992 was 262 mm, the range being from 183 mm to 425 mm with a coefficient of variation (CV) of 25%. On a longer span of time (20 rainfall years recorded between 1957 and 1981) the CV exceeded 35% (Dennett *et al.*, 1984). Rainfall, which is low on average and variable from year to year, occurs invariably between October and May coinciding, therefore, with the crop cycle of winter cereals. Most precipitation falls during the cold winter months and to a lesser extent during the warmer spring months. Details of the origin of rainfall events in this area have been given by Perrin de Brichambaut and Wallén (1963). The rainfall year is taken as August to July. The mean number of raindays with rainfall >2 mm is 30, with mean rain per rainday of 8.7 mm. There is little probability (less than one in four years) of having a total seasonal rainfall exceeding 300 mm and a total number of raindays greater than 35 (Figures 5a and 5b). The overall probability or rain throughout the year is shown in Figure 5c. January is the wettest month, followed by February and December. Figure 5d shows that the risk of having a dry spell of at least 10 days during the 20 days following a rainy day is high, particularly during the early part of the season. This risk may affect important agricultural decisions such as sowing

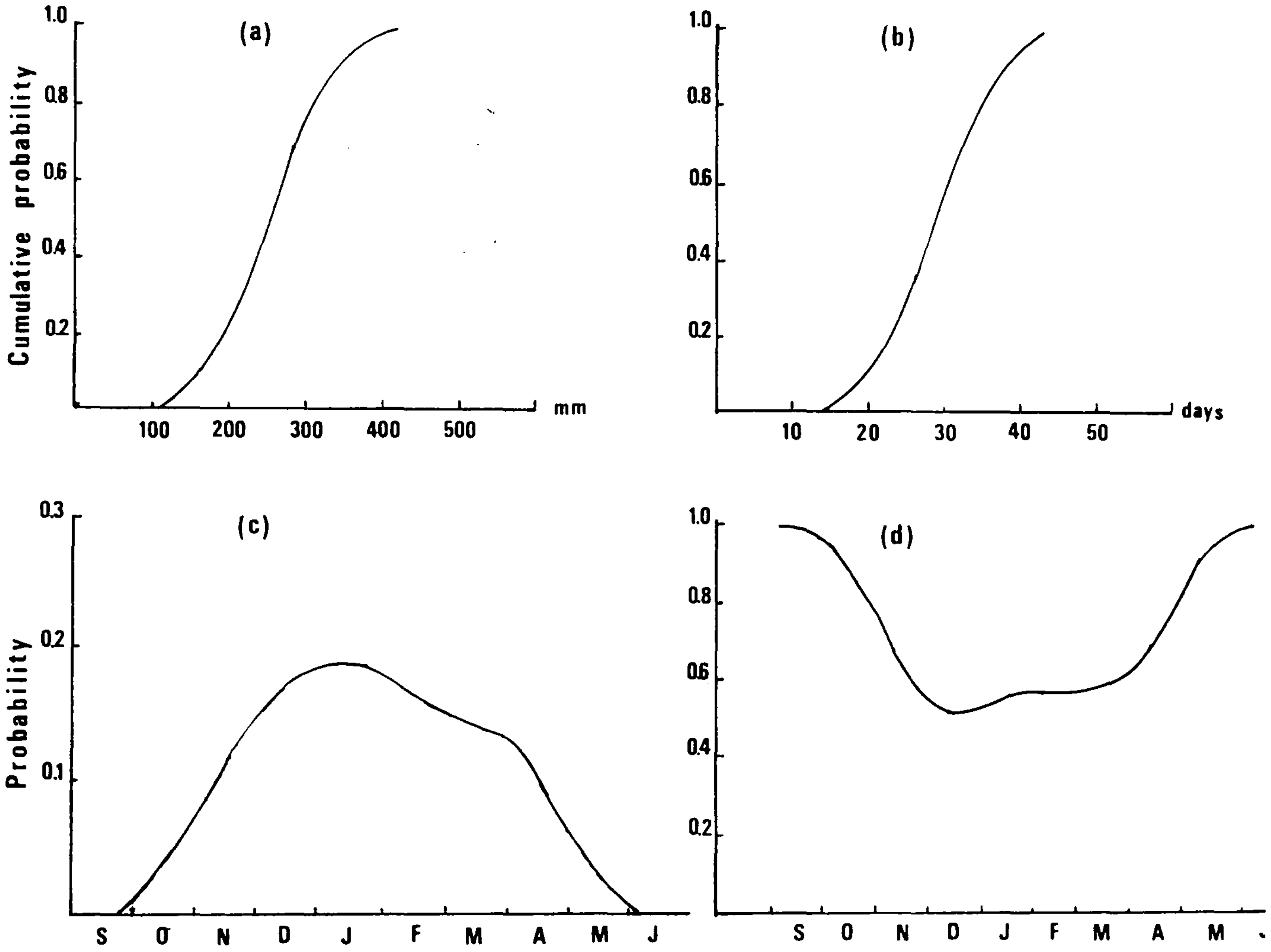


Figure 5. Rainfall parameters relative to Breda, northern Syria: a) cumulative probability distribution of seasonal total rainfall (August to July); b) cumulative probability distribution of seasonal number of raindays; c) overall probability of rain throughout the year; d) probability of a dry spell of at least 10 days during the subsequent 20 days following rain on the date on the time axis. From: Dennett *et al.* (1984).

date. Early planting is desirable as it extends the effective growth period of the crop, thereby conferring a yield advantage which is further increased by a higher water-use efficiency, as early planted crops develop a closed canopy more rapidly, reducing evaporation from the soil surface. Early planting, however, may also increase the risk of damage by drought in the early growth stages. Simulation models show that the probability of a long dry spell during the seedling stage in the area around Breda is about 40% assuming that germination had occurred by 1 November, and 10-20% for a germination occurring by 1 December (ICARDA, 1990, Figures 2 and 3). For this reason mid-November to mid-December sowing dates are typical for the study area (Stapper and Harris, 1989).

Temperature also plays an important role in restricting plant growth at two stages of the season. During the cold winter months (December, January, February) temperatures are sub-optimal for crop growth and occasional frost damage may occur, while in late April-May there is a rapid increase in temperatures which reach super-optimal levels during the period of crop maturity (Cooper *et al.*, 1987). These high temperatures coincide with the end of the rains and are accompanied by a sharp increase in evaporation rates. The final stage of crop growth (grain filling) invariably takes place in conditions of water and high temperature stress. The hottest month is July with a mean maximum daily temperature of 37.1° C, while the coldest is January with a mean minimum daily temperature of 1.5° C. On average (period 1980-1992) there were 44 frost days per season, with a minimum of 34 and a maximum of 72. The lowest recorded absolute minimum temperature was -9.6° C. There exists a high probability (about 50%) of frost occurring after the commencement of stem elongation (ICARDA, 1992), and even some probability (5-10%) of frost during the very sensitive phase between heading and the start of linear grain filling (ICARDA, 1991). The effect of frost at these stages on crop grain yield is much more severe than that of frost at earlier stages of crop growth (Harris *et al.*, 1987).

In seven seasons out of 12 between 1980 and 1992 the latest frost day has occurred after 15 March, i.e., when winter cereals are likely to be in the elongation phase. In three of these seven cases the latest frost was recorded after 1 April, that is, a date when cereal plants are in the booting stage and close to heading.

Crop yield responses are very variable in Breda as a result of the varying climatic conditions, especially rainfall. The minimum rainfall requirement for wheat grain production in the study area was estimated to be 130 mm, with an average yield increase of 1.4 g m^{-2} for each additional 1-mm rainfall (Stapper and Harris, 1989). Actual data from the locality show that grain yield of durum wheat advanced breeding lines ('Advanced yield trials') varied across six seasons from a minimum of 494 kg ha^{-1} in a season with 179 mm rainfall to a maximum of 3608 kg ha^{-1} in a season with 408 mm. The control cultivar 'Haurani' ranged between 503 kg ha^{-1} and 3066 kg ha^{-1} in the same seasons (Nachit *et al.*, 1992).

Breda is also useful to widen the range of rainfall under which germplasm evaluation is carried out in studies on yield stability within the target Mediterranean region (Annicchiarico and Pecetti, 1993; Pecetti and Annicchiarico, 1993). Its soil characteristics also allow the testing of cereal germplasm at a low level of fertility within the target area. Soil at Breda is classified as Calcic Xerosol (according to the FAO-UNESCO nomenclature) or Typic Calciorthid (according to the USDA soil taxonomy). Total depth above the substratum is about 1 m. The parental material is made up of residuum from limestone, probably mixed with colluvial or other transported materials. The 0-25 cm layer is a dull reddish brown clay loam (30% clay, 45% silt, 25% sand). It has a moderate angular blocky structure, and aggregates occur in all sizes due to ploughing. The soil aggregates contain many fine pores which allow a rapid infiltration of rainwater and deeper distribution. Throughout the profile some rounded-off stones occur, up to 10 cm in size, representing less than 5% of the soil volume. Consistency of dry soil is hard.

The arid climate with long, hot and dry summers, keeps the organic matter content low but encourages the accumulation of calcium carbonate and the fixation of phosphate as insoluble calcium compounds. The soil at Breda is typically calcareous with a $CaCO_3$ content of 30% in the top layer and up to 56.5% at depth. The soil top layer has an organic matter content of 1.2 (w/w), a pH of 8.3 which increases slightly with depth, and an electrical conductivity (EC_e) of 0.3 dS m^{-1}. Crop available nitrogen derives from the mineralisation of soil organic matter, so that, in general, the less organic matter the less nitrogen is likely to be made available. Total mineral nitrogen (NO_3^- and NH_4^+) in the top soil is low (<50 kg ha^{-1}). Most soil phosphate is held in mineral form. In calcareous soils, these minerals are highly insoluble materials that maintain only low concentrations of phosphate ions in the soil solution and release phosphate only slowly as that solution is depleted by crop uptake. The available-P (Olsen method) content in Breda is less than 6 ppm. All the preceding information was obtained either from ICARDA (1981) or by a personal communication of Dr. A. Matar, ICARDA Soil Chemist.

2.2 *Methods*

Out of the total number of accessions selected from the ICARDA collection on the basis of their high agronomic score (7 to 9) recorded during the collection evaluation (Pecetti and Annicchiarico, 1991), the apparently best 25 accessions underwent two cycles of further evaluation in very dry seasons (1988-89 and 1989-90) at Breda. A set of morpho-physiological characters was recorded together with grain yield with the following aims: i) to compare the relative performance of the selected accessions in the two consecutive dry seasons of evaluation; ii) to assess differences for characters of agronomic importance among the selected accessions in both seasons and identify possible different character architectures, resulting in a similar performance under drought.

In the second season of evaluation a set of 50 accessions randomly taken from the collection was included, 25 of which rated with an intermediate score (4 to 6) and 25 rated with a low score (1 to 3). The ratio 1:2 between selected and randomly taken accessions was chosen as it represented the ratio existing between the number of score levels considered for selection (3) and the number of non-selected score levels (6). The further aims of the evaluation were: iii) ascertaining whether accessions selected for their agronomic score confirmed their superiority also in terms of grain yield when grown under severe stress conditions in comparison with non-selected materials; iv) testing whether or not these selected accessions, on average, proved different for a set of agronomic traits from the non-selected materials. Given the wide range of expected performance (on the basis of the preliminary evaluation results (Pecetti and Annicchiarico, 1991)), in the second season a selection simply based on the actual grain yield was also conceived. Selected accessions for grain yield were compared with the remaining entries in order to try to understand possible reasons for different performance under stress.

During the two seasons the total annual rainfall was particularly below the average, reaching only 194 mm and 183 mm, respectively. Rainfall distribution was also very uneven. The season 1988-89 had a start with ample, much higher than average rainfall followed by a long, very dry second period. By the end of December 85% of the total rainfall had fallen, that is, very little rain occurred during the most crucial phases of the crop cycle (Figure 6). The following season started with good rains falling in distinct spells between mid-November and mid-December. The rest of December and January were rather dry, while there was significant precipitation during February. No substantial rain was recorded after that (Figure 6).

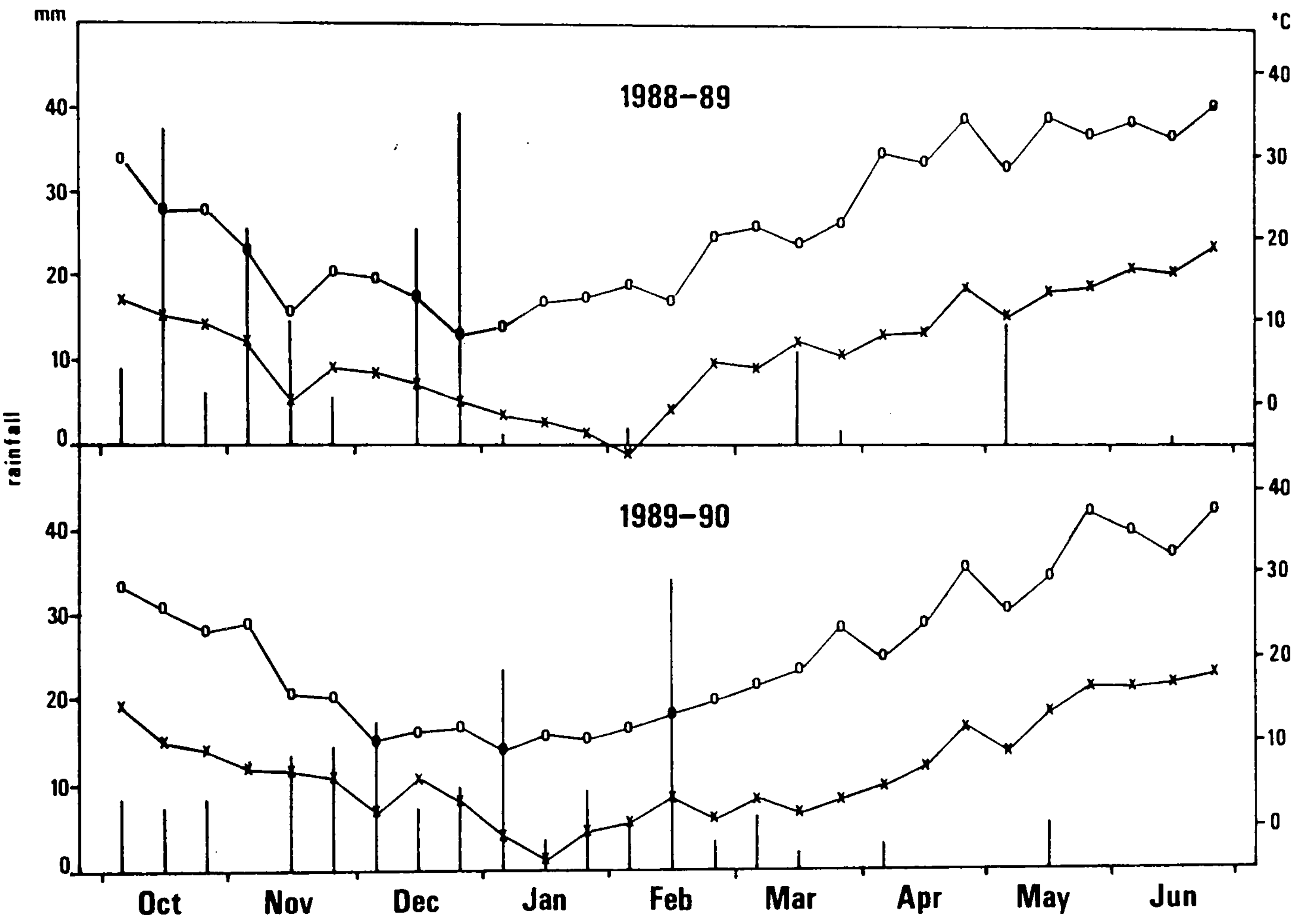


Figure 6. Ten-day rainfall (|), average daily maximum (—o—) and minimum (—x—) temperature in 1988-89 and 1989-90 at Breda, northern Syria.

The two seasons were also noticeably cooler than average, confirming that low and variable rainfall and low temperatures during canopy development with the possibility of frost are associated features of the environment under consideration (Acevedo, 1987). Fifty-two and 49 frost days occurred during the two seasons, markedly above the average, with an absolute minimum temperature of -9.4° C recorded on 2 February in the first season and -7.2° C recorded both on 10 January and 17 March in the second season. While the first season was characterized by a prolonged frost spell from the end of December through mid-February, in the second season a frost spell in January and, partly, February was followed by a short but very damaging spell around mid-March (Figure 6). This second frost event occurred when wheat plants were already in the booting stage and had a remarkable consequence on spike fertility, thus confounding its effect with the drought effect.

In both seasons the experiments were sown in the last decade of November and harvested in the first decade of June. The harvested plot size was 3 m^2 (4 rows, 2.5 m long, 30 cm apart, seed rate of about 250 seeds m^{-2}); fertilization rate, applied prior to sowing, was 40 kg ha^{-1} of N plus 40 kg ha^{-1} of P_2O_5. In 1988-89 the 25 entries were planted according to a simple lattice design with two replications; in 1989-90 the 75 entries were sown in a randomised complete block design with three replications.

A set of characters was recorded in each season as follows:

- *days to emergence* (recorded only in 1989-90): counted from the date of the first sufficient rainfall for germination to when 50% of the seedlings had emerged in the plot;
- *early growth vigour* (recorded in both seasons): scored using the scale 1 (very poor) - 3 (poor) - 5 (intermediate) - 7 (good) - 9 (very good);
- *frost damage* (recorded in both seasons): scored in February in both seasons using the scale 1 (no visible damage or just traces) - 2 (less than 25% plants with

some damage) - 3 (up to 50% damaged plants) - 4 (more than 50% damaged plants) - 5 (more than 75% damaged plants). No damage score could be recorded in March at Breda during 1989-90, whereas it was recorded on the same materials at the nearby station of Tel Hadya. The correlation coefficient between the score recorded at Breda in February and the one recorded at Tel Hadya in March was highly significant. Therefore the only score recorded at Breda should also provide a reliable indication of the tolerance against later occurring frost events;

- *days to heading* (recorded in both seasons): counted from the date of the first sufficient rainfall for germination to when 50% anthesis in the plot occurred.
- *days to maturity* (recorded in both seasons): counted from the date of the first sufficient rainfall for germination to when 50% physiological maturity (yellowed uppermost internode) (Ceccarelli and Grando, 1989) in the plot occurred;
- *plant height* (recorded in both seasons): measured at maturity from the ground to the spike tip, excluding the awns;
- *peduncle length* (recorded in both seasons): measured at maturity;
- *number of spikes per unit area* (recorded in both seasons): scored using the scale 1 (low) - 3 (fair) - 5 (high) in 1988-89; counted in a quadrat of 0.6 m x 0.6 m in 1989-90;
- *spike length* (recorded only in 1988-89): measured at maturity from the basal spikelet to the tip, excluding the awns;
- *number of kernels per spike* (recorded only in 1988-89): average of counts made on three spikes randomly taken from each plot;
- *1000-kernel weight* (recorded only in 1988-89): measured on a sample of kernels randomly taken from each plot;
- *grain yield* (recorded in both seasons): measured in grams plot^{-1}.

2.3 *Results*

Overall mean values of the 25 selected accessions for the characters recorded are shown in Table 4. In general, the genetic base of the 25 entries seemed broad enough to ensure a sufficiently large variability for most of the considered traits. The F-test results from ANOVA of these traits recorded on the 25 selected accessions in the two seasons are summarised in Table 5. The 25 entries differed significantly for all traits, except for peduncle length in both seasons. It is likely that early growth vigour was subject to genotype-season interaction, as the accessions differed significantly for this character only in 1988-89.

A comparison of entry mean yields was made in both seasons and the separation of the highest and lowest ranking entries is reported in Table 6. Five accessions, as indicated in Table 6, ranked best in both seasons, and three appeared at the bottom. Mean values of these two groups of five and three entries were compared by an ANOVA for all characters recorded in the two seasons, except yield. The results, shown in Table 7, revealed that the group of the five top entries was, on average, earlier in heading and maturity and shorter in stature than the group of the three bottom accessions in both seasons. Although the difference in plant height may be due to the particular set of materials involved, the result suggests that a good performance under drought stress is not necessarily related to tall stature. In 1989-90 the top group was also more frost tolerant than the bottom group, suggesting that in that season the better ability to withstand the frost gave an advantage in terms of final performance.

In an attempt to explore possible different plant architectures and agronomic models resulting in similar performance, the variation among the five top accessions for the traits recorded in both seasons was tested by ANOVA. For those characters showing significant ($P \leq 0.05$) variation, entry means were compared by Duncan's multiple range test (Duncan, 1955). The results showed distinct features of some of the five top entries (Table 8). Accession '10926' was characterised by a constant earliness in heading and, particularly, maturity. It could be therefore classified as a true drought "escaper". Its mechanism of stress escape was accompanied by reduced tillering. Entry '37499' had a short stature in both seasons (although in 1988-89 entry differences did not result significant). Its good performance could be attributed to a relatively high harvest index. The results of entry '83089' suggested the presence of a relatively high number of fertile tillers associated with lateness. This may be a drought tolerant accession able to maintain a high 'sink' capacity even in the presence of the stress. The mean values of entry '37565' in 1988-89 indicated a long grain filling period as a result of early heading and delayed maturity. This entry in 1989-90 tended to be early and with a high number of fertile tillers. Entry '83022' was characterised by late cycles in both seasons, tall stature in 1988-89, and high number of fertile tillers in 1989-90. These traits suggested a certain level of stress tolerance in this accession.

Correlation coefficients between grain yield and the other recorded characters for the 25 selected entries in the two seasons are reported in Table 9. It is evident that a positive correlation consistently occurred between grain yield and peduncle length, while a negative correlation was present between yield and both heading and maturity date. Of the traits recorded only in 1988-89, number of kernels per spike showed a remarkable correlation with yield. This result is consistent with the findings of another study on durum wheat germplasm (Annicchiarico and Pecetti, 1993) where kernel number has proved one of the best predictors for yield performance and stability, and the only yield component strongly related to the performance. Quite surprisingly, frost tolerance was highly related to yield in 1988-89 but not in 1989-90 although in that season a significant difference in frost tolerance was detected between the best and worst yielding entries (see

Table 4. Overall mean value of the characters recorded at Breda in 1988-89 and 1989-90 on 25 durum wheat entries previously selected on the basis of their agronomic score.

	1988-89	1989-90
Character	Mean (± s.e.)	Mean (± s.e.)
Yield (g plot^{-1})	222.2 ± 11.8	127.6 ± 7.9
Early growth vigour (1-9)	4.4 ± 0.2	5.8 ± 0.1
Frost damage (1-5)	2.3 ± 0.1	1.8 ± 0.1
Days to heading (dd.)	145.3 ± 0.7	146.9 ± 0.5
Plant height (cm)	55.6 ± 1.5	38.7 ± 1.1
Days to maturity (dd.)	171.3 ± 0.8	172.2 ± 0.7
Peduncle length (cm)	19.8 ± 0.6	11.1 ± 0.3
Tillering[a]	3.4 ± 0.3	139.9 ± 4.3
Spike length (cm)	6.1 ± 0.1	- -
Kernels per spike (no.)	20.3 ± 1.0	- -
1000-kernel weight (g)	29.3 ± 0.5	- -
Days to emergence (dd.)	- -	16.3 ± 0.2

[a] scale 1-5 in 1988-89, number of spikes in a sample area of 3600 cm^2 in 1989-90.

Table 6. Mean separation of highest and lowest ranking entries for grain yield at Breda in 1988-89 and 1989-90. Entries in bold are among the best and worst yielding in both seasons.

1988-89		1989-90	
Entry	Yield (g plot^{-1})	Entry	Yield (g plot^{-1})
38552	315.0 a	**37565**	208.0 a
37565	307.0 a	**10926**	201.0 a
83022	282.0 a	**37499**	179.3 a
7638	274.5 a	83008	176.0 a
83005	267.5 a	**83022**	160.0 a
83063	259.5 a	M21	153.3 a
9256	258.0 a	M13	152.7 a
83089	258.0 a	**83089**	145.7 a
9245	257.5 a	9256	132.3
10926	256.5 a	83104	131.0
37499	249.5 a	7638	129.3
9282	246.5 a	83005	126.0
83011	240.5 a	38552	122.0
83104	233.0 a	9282	121.3
M13	217.0	9705	120.0
83008	210.0	9245	120.0
9408	209.0	83063	117.0
9705	207.0	9408	111.3
5971	185.5	83011	109.3
12257	182.0 b	4727	109.0
M21	180.0 b	5971	93.0
4727	129.0 b	9278	86.7 b
9278	117.5 b	**12257**	79.0 b
5694	116.0 b	**5695**	77.0 b
5695	97.5 b	**5694**	30.7 b

Means followed by the same letter within columns are not different at $P \leq 0.05$, according to Duncan's multiple range test.

Table 7. Comparison of character mean values between the group of five Top entries and the group of three Bottom entries across the two seasons at Breda.

	1988-89				1989-90		
Character	Top		Bottom	Character	Top		Bottom
Early vigour (1-9)	4.8	ns	3.7	Early vigour (1-9)	5.9	ns	5.7
Frost damage (1-5)	2.1	ns	2.7	Frost damage (1-5)	1.3	***	2.4
Days to heading (dd.)	143.4	**	151.7	Days to heading (dd.)	146.3	*	149.8
Plant height (cm)	54.2	*	68.3	Plant height (cm)	37.9	*	49.3
Days to maturity (dd.)	170.6	**	178.3	Days to maturity (dd.)	171.5	**	177.8
Tillering (1-5)	3.2	ns	3.0	Tillering (no.)	131.6	ns	116.8
Spike length (cm)	5.9	*	6.9	Days to emerg. (dd.)	16.5	ns	16.3
Kernels/spike (no.)	21.4	ns	17.3	Peduncle length (cm)	12.5	ns	11.9
1000-kern. weight (g)	30.8	ns	30.6				
Peduncle length (cm)	20.0	ns	21.5				

ns, *, ** and ***: group means not different, different at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively, according to ANOVA.

Table 8. Entry mean values of the characters for which the five top yielding entries (across the two seasons of evaluation at Breda) differed significantly ($P \leq 0.05$) among themselves in each season, according to ANOVA.

Entry	1988-89	1989-90
	Tillering capacity (scale 1-5)	Number of fertile tillers
83089	5 a	135.7 a
83022	3 b	150.3 a
37499	3 b	135.3 a
37565	3 b	133.7 a
10926	3 b	103.0 b
	Days to heading	Days to heading
83089	146.0 a	147.3 a
83022	145.5 a	148.3 a
37565	142.0 b	144.3 b
37499	142.0 b	148.0 a
10926	141.5 b	143.3 b
	Days to maturity	Days to maturity
37565	173.0 a	171.0 bc
37499	171.5 a	171.3 bc
83089	171.0 a	172.0 ab
83022	171.0 a	174.7 a
10926	166.5 b	168.7 c
		Plant height
10926		41.3 a
83022		40.7 ab
37565		39.3 ab
83089		35.3 bc
37499		32.7 c

Means for each character in each season followed by the same letter are not different at $P \leq 0.05$ according to Duncan's test.

Table 9. Ranking of the correlation coefficients (r) for the 25 selected entries between grain yield and the other recorded characters in the two seasons at Breda.

1988-89		1989-90	
Character	r	Character	r
Days to heading	-0.64 ***	Peduncle length	0.49 **
No. kernels/spike	0.52 **	Days to heading	-0.43 *
Peduncle length	0.47 *	Days to maturity	-0.43 *
Days to maturity	-0.45 *	No. of tillers	0.18 ns
Frost damage	-0.42 *	Frost damage	-0.14 ns
Tillering capacity	0.32 ns	Days to emergence	-0.07 ns
Early growth vigour	0.24 ns	Plant height	0.02 ns
Spike length	-0.17 ns	Early growth vigour	0.00 ns
Plant height	0.15 ns		
1000-kern. weight	-0.04 ns		

ns, *, ** and ***: not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 7).

Table 10 reports the overall mean values for the characters recorded in 1989-90 on the set of 75 accessions. The comparison for all characters between the groups of selected and non-selected (randomly taken) entries evaluated in that season is shown in Table 11. Selected entries clearly outyielded non-selected materials. The yield advantage percentage of the selected group (+ 117%) was even higher than previously reported for a similar experiment (Annicchiarico and Pecetti, 1990). The two groups of materials also differed greatly in terms of peduncle length, heading time and maturity time. Other significant differences included frost damage and date of emergence.

For each group of entries, correlation coefficients between yield and other traits were computed and ranked in Table 12. Irrespective of the group performance, the characters most closely related to grain yield were peduncle length, days to heading and to maturity, the two latter traits having a negative correlation with yield.

For all 75 accessions evaluated in 1989-90, an ANOVA was carried out testing variability among entries for grain yield. Highly significant differences ($P \leq 0.001$) were detected, confirming that altogether the 75 accessions represented a set of materials with very varying response to the stress. The best ranking entries, not differing significantly ($P \leq 0.05$) from each other, were identified by the Newman and Keuls test. In this thesis, multiple comparisons of treatment means were usually carried out by the above-mentioned Duncan's multiple range test. However, in some cases, such as the present analysis, the more conservative Newman and Keuls test of multiple comparison of means (Steel and Torrie, 1960; Snedecor and Cochran, 1972) has been used. Two mean values separated by this test, even at a probability level of 5%, have very little chance of not being really different. The best yielding entries in 1989-90, separated by the test, are reported in Table 13. Given the great importance attributed to earliness for good perfor-

Table 10. Overall mean value of the characters recorded at Breda in 1989-90 on 75 durum wheat entries.

Character	Mean (± s.e.)
Yield (g plot^{-1})	81.7 ± 5.7
Early growth vigour (1-9)	5.7 ± 0.1
Frost damage (1-5)	2.2 ± 0.1
Days to heading (dd.)	148.5 ± 0.2
Plant height (cm)	38.4 ± 0.6
Days to maturity (dd.)	175.0 ± 0.5
Peduncle length (cm)	9.9 ± 0.2
Fertile tillers (no.)	148.1 ± 3.2
Days to emergence (dd.)	15.9 ± 0.1

Table 11. Comparison of character mean values between the group of 25 selected entries (S) and the group of 50 non-selected (NS) entries. Breda 1989-90.

Character	Mean		
	S		NS
Yield (g plot^{-1})	127.6	***	58.8
Early vigour (1-9)	5.7	ns	5.6
Peduncle length (cm)	11.1	***	9.3
Days to heading (dd.)	146.9	***	149.3
Days to maturity (dd.)	172.2	***	176.5
Fertile tillers (no.)	152.2	ns	139.9
Frost damage (1-5)	1.8	**	2.4
Days to emergence (dd.)	16.3	**	15.7
Plant height (cm)	38.7	ns	38.2

ns, ** and ***: group means not different, different at P ≤ 0.01 and P ≤ 0.001, respectively, according to ANOVA.

Table 12. Ranking of the correlation coefficients (r) for the 25 selected entries (S) and for the 50 non-selected entries (NS) between grain yield and the other characters recorded in 1989-90 at Breda.

S			NS		
Character	r		Character	r	
Peduncle length	0.49	**	Days to maturity	-0.46	***
Days to heading	-0.43	*	Days to heading	-0.45	***
Days to maturity	-0.43	*	Peduncle length	0.44	***
Fertile tillers	0.18	ns	Plant height	0.23	ns
Frost damage	-0.14	ns	Frost damage	-0.16	ns
Days to emergence	-0.07	ns	Fertile tillers	0.13	ns
Plant height	0.02	ns	Days to emergence	-0.07	ns
Early growth vigour	0.00	ns	Early growth vigour	0.06	ns

ns, *, ** and ***: not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 13. Accession number and mean grain yield of the best yielding entries (out of the total 75 entries) at Breda in 1989-90.

Accession number	Grain yield (g $plot^{-1}$)
37565	208.0
10926	201.0
37499	179.3
83008	176.0
7178	166.7
7419	163.3
83022	160.0
M21	153.3
M13	152.7
7331	150.0
83089	145.7

Means are not different at $P \leq 0.05$ according to the Newman and Keuls test.

mance under drought stress (e.g., Turner, 1979), the earliest entries for both heading and maturity time were identified by the Newman and Keuls test, as reported in Table 14. Comparing the accessions listed in Table 14 with the best yielding ones in Table 13, it is evident that not all the best performing entries are also among the earliest ones, nor vice-versa. Seven entries were earliest in both heading and maturity, and of these only four were also top-yielding. For these four entries drought escape must clearly play a major role, contributing to their good performance. Entries '37565' and '7178' were among the earliest in heading but not in maturity: this might mean that they were able to delay senescence during the critical phase of grain filling. Entries '37499', '83022', '83089' and '83008' owe their performance to attributes other than earliness. In particular, for the three former entries the performance of both 1988-89 and 1989-90 has been previously discussed in the comment of Table 8, where an optimal harvest index has been suggested for '37499' and drought tolerance for '83022' and '83089' (both Jordanian landraces). It is likely that '83008', being another Jordanian landrace, has a similar tolerance level. Thus, earliness is not the only mechanism involved in good performance under drought. However, its role is of paramount importance, as demonstrated by the values reported in Table 15, where the seven earliest entries for both heading and maturity (shown in Table 14) were compared to the 46 latest entries for all considered traits. Grain yield of the earliest group was 2.7-fold higher than that of the latest group. It is also noticeable that the only other character for which the two groups differed is peduncle length.

The best yielding entries listed in Table 13 were compared with the remaining accessions for all recorded characters. The results of this comparison, reported in Table 16, showed that the top-yielding entries greatly differed from all others for peduncle length, heading and maturity time, and frost damage. As also reported in the case of the comparison based on the visual score (Table 11), the best performing accessions differed from the others for the emergence date, the

Table 14. Accession number and number of days to heading (DHE) and to maturity (DMA) of the earliest entries (out of the total 75 entries) at Breda in 1989-90.

Accession number	DHE	Accession number	DMA
7419 +	143.0	**M21** +	166.0
M21 +	143.0	**M13** +	166.3
M13 +	143.3	**4727**	167.3
10926 +	143.3	7168	167.7
7638	143.7	**38552**	168.0
38552	144.0	7331 +	168.0
37565 +	144.3	**10926** +	168.7
7178 +	144.7	7274	169.0
9282	144.7	**9282**	169.3
4727	145.0	7491	169.7
		7267	169.7
		7419 +	169.7
		7529	169.7
		9256	170.3
		9705	170.3
		7237	170.7

For each character, means are not different from each other at $P \leq 0.05$ according to the Newman and Keuls test.

Entries in bold are in common to both lists.

+ : entries also included in the best yielding group (see Table 13).

Table 15. Comparison of character mean values between the group of 7 earliest entries (Early) and the group of 46 latest entries (Late). Breda 1989-90.

Character	Mean		
	Early		Late
Yield (g $plot^{-1}$)	146.1	***	54.6
Early vigour (1-9)	5.7	ns	5.6
Peduncle length (cm)	11.4	*	9.5
Days to heading (dd.)	143.8	***	149.8
Days to maturity (dd.)	167.9	***	178.0
Fertile tillers (no.)	142.1	ns	145.6
Frost damage (1-5)	2.0	ns	2.4
Days to emergence (dd.)	16.4	ns	15.8
Plant height (cm)	36.5	ns	39.9

ns, ** and ***: group means not different, different at $P \leq 0.01$ and $P \leq 0.001$, respectively, according to ANOVA.

Table 16. Comparison of character mean values between the group of 11 best yielding entries (Top) and the group of the remaining entries (Rest). Breda 1989-90.

Character	Mean		
	Top		Rest
Yield (g $plot^{-1}$)	168.7	***	66.8
Early vigour (1-9)	5.7	ns	5.7
Peduncle length (cm)	11.8	***	9.6
Days to heading (dd.)	145.6	***	149.0
Days to maturity (dd.)	170.1	***	175.9
Fertile tillers (no.)	143.8	ns	148.8
Frost damage (1-5)	1.7	**	2.3
Days to emergence (dd.)	16.3	*	15.8
Plant height (cm)	36.5	ns	38.7

ns, ** and ***: group means not different, different at $P \leq 0.01$ and $P \leq 0.001$, respectively, according to ANOVA.

former emerging about half a day later.

The correlation coefficients between grain yield and the other traits recorded in 1989-90 for the two groups of top-yielding and remaining entries are ranked in Table 17. In the best entry group only peduncle length was significantly ($P \leq 0.05$) correlated with grain yield, whereas in the remaining entry group there was an evident correlation with earliness and, to a minor extent, with frost damage, peduncle length and time to emergence.

The 11 top entries were subject to ANOVA for all considered traits. Differences were significant ($P \leq 0.05$) for all characters except peduncle length and early growth vigour (data not shown). Entry mean separation of the variables for which the 11 accessions significantly differed are reported in Table 18. It was possible to identify differences among the best yielding entries in terms of character combinations. For instance, entry '7419' was characterised by a certain frost susceptibility, but its early heading, accompanied by a relatively long grain filling period and a reduced number of spikes, must have accounted for its good yield. It is difficult to attribute any meaning to its relatively long period from sowing to seedling emergence. Entries 'M21' and 'M13', two Moroccan landraces, were similar in plant structure: both relied on their distinct earliness, especially in terms of maturity, which is a common feature in the Moroccan germplasm (Pecetti *et al.*, 1992a). However, they were also able to maintain a relatively high number of fertile tillers. Entry '83022' is a typical example of a drought and, probably, frost tolerant accession, characterised by lateness, tall plant stature and low frost susceptibility even to late occurring events (according to data recorded at Tel Hadya). It would be important to verify whether this entry would perform as well in environments where the drought stress is not associated with a frost stress. Similar behaviour was shown by entries '83089' and '83008' except for their relatively lower plant height. Entry '10926', as previously discussed in relation to data in Table 8, tended to escape the stress, had relatively tall plant stature and

Table 17. Ranking of the correlation coefficients (r) for the 11 best yielding entries (Top) and for the remaining entries (Rest) between grain yield and the other characters recorded at Breda in 1989-90.

Top		Rest	
Character	r	Character	r
Peduncle length	0.60 *	Days to maturity	-0.63 ***
Plant height	0.53 ns	Days to heading	-0.57 ***
Early growth vigour	0.52 ns	Frost damage	-0.37 **
Fertile tillers	-0.43 ns	Peduncle length	0.34 **
Frost damage	-0.31 ns	Days to emergence	0.28 *
Days to heading	-0.18 ns	Early growth vigour	0.12 ns
Days to maturity	0.17 ns	Plant height	-0.05 ns
Days to emergence	0.14 ns	Fertile tillers	0.00 ns

ns, *, ** and ***: not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 18. Top (=best yielding) entry means and mean separation of the characters for which the Top entries differed significantly ($P \leq 0.05$) according to ANOVA. Breda 1989-90.

Frost damage (1-5)		Days to heading (dd.)		Days to maturity (dd.)		Plant height (cm)		Fertile tillers (no.)		Days to emergence (dd.)	
Entry	Mean	Entry	Mean	Entry	Mean	Entry	Mean	Entry	Mean	Entry	Mean
7419	2.7 a	83022	148.3 a	83022	174.7 a	10926	41.3 a	7178	198.7 a	7419	18.0 a
M21	2.3 ab	83008	148.3 a	83089	172.0 ab	83022	40.7 a	M21	162.0 b	83089	17.0 ab
7178	2.0 abc	37499	148.0 ab	83008	172.0 ab	37565	39.3 ab	M13	160.3 b	10926	17.0 ab
M13	2.0 abc	7331	147.7 ab	7178	171.3 ab	7178	38.0 ab	7331	157.7 b	83008	17.0 ab
7331	1.7 bcd	83089	147.3 ab	37499	171.3 ab	83008	36.3 abc	83022	150.3 b	37499	17.0 ab
83008	1.3 cd	7178	144.7 abc	37565	171.0 ab	M13	36.0 abc	83008	141.3 b	M21	16.3 ab
37499	1.3 cd	37565	144.3 bc	7419	169.7 bc	7419	35.7 abc	83089	135.7 bc	37565	16.0 bc
37565	1.3 cd	M13	143.3 c	10926	168.7 bc	M21	35.3 abc	37499	135.3 bc	83022	15.7 bc
83022	1.3 cd	10926	143.3 c	7331	168.0 bc	83089	35.3 abc	37565	133.7 bc	M13	15.7 bc
10926	1.3 cd	M21	143.0 c	M13	166.3 c	37499	32.7 bc	7419	103.3 c	7331	15.7 bc
83089	1.0 d	7419	143.0 c	M21	166.0 c	7331	31.0 c	10926	103.0 c	7178	14.3 c

For each character, means followed by the same letter are not different at $P \leq 0.05$ according to Duncan's test.

low number of fertile tillers. Conversely, entry '7178' possessed a very high number of spikes together with a certain lateness and a medium frost tolerance. This entry could therefore be indicated as, somewhat, drought tolerant (in a broad sense). Entry '7331' is a possible drought "escaper" due to its early maturity; the number of spikes is fairly high, while the plant height is low, suggesting a possible high harvest index. A high harvest index is also likely for entry '37499', as previously suggested also by Table 8.

2.4 *Discussion*

The data presented above show that the 25 selected accessions formed a variable pool of durum wheat germplasm, of diversified geographic origin (11 countries were represented). The existing variability was obviously amplified by the inclusion, in the second season, of less adapted materials. In 1989-90, 19 countries were represented altogether: six countries in both the selected and the non-selected groups, eight only in the non-selected group, and five (Syria, Jordan, Morocco, Chile and France) only in the selected one. Variability might be very desirable in breeding activities for drought tolerance, as genetic diversity for key physiological processes or for morphological traits may be lacking in present improvement programmes, so that important genes may not be available for selection to act (Richards, 1989). If the objective was to evaluate and validate the potential of a trait, Richards (1989) also stated that testing a substantial number of diverse homozygous genotypes would be an alternative to the use of near-isogenic lines. Acevedo and Ceccarelli (1989) did not consider the use of near-isogenic lines the most satisfactory methodology for trait verification because it only generates information on the effect of a particular trait in a particular genetic background. The diversity of the material under test, though introducing complexity to the analysis, avoids bias associated with the nursery.

The adopted visual score in the selection of durum wheat for drought tolerance (Annicchiarico and Pecetti, 1990) confirmed its value also in dry seasons other than the one of the preliminary evaluation. The selected accessions on the basis of the score indeed outyielded by far the non-selected entries in 1989-90 (Table 11). Of the other characters for which the two groups differed, earliness had been consciously selected for according to the score definition (Annicchiarico and Pecetti, 1990), while peduncle length and frost tolerance must have been traits related to the overall accession appearance and performance. No apparent meaning could be ascribed to the difference between selected and non-selected entries for time of seedling emergence. The same difference was also noticed between top-yielding and remaining entries (Table 16). Whether this is due either to a slower germination or to a shorter coleoptile of the better performing germplasm would perhaps deserve further observations. Allan *et al.* (1962) found a positive correlation among seedling emergence rate, coleoptile length and plant height in a large set of bread wheat selections differing for plant stature. In the present study different combinations of plant height and emergence date of 50% seedlings occurred. There were entries with rather short stature and rather late emergence ('37499' and '83089') and, vice-versa, entries with rather tall plants and rather fast emergence ('83022' and '7178'). Both these combinations confirmed the findings of Allan *et al.* (1962). But entries with tall stature and slow emergence ('10926') or short plants and fast emergence ('7331') were also observed. Similar exceptions to the generalised behaviour had already been evidenced by Allan *et al.* (1962).

One clear feature emerging from the present study is the paramount importance of earliness, at any level it was considered in selecting durum wheat under drought conditions (Tables 7, 9, 11, 12, 14, 15 and 16). Many are the examples quoted in the literature about the importance of earliness in ensuring a good yield performance of durum wheat under moisture-limiting conditions (e.g. Fischer and Maurer, 1978; Acevedo, 1991; Annicchiarico and Pecetti, 1993). Morgan (1989) and Richards (1989) saw the development of faster maturing types as the basic drought escape mechanism to better match the water demand to water supply. This means modifying crop phenology so that the most sensitive growth periods avoid the most severe stress periods. Clarke (1987) regarded early maturity as one of the water conservation mechanisms important when the crop is grown under conditions of limited water supply and continually increasing stress. That would have been the case of the two seasons considered in the present study, given their low and uneven rainfall distribution. Harris *et al.* (1987) stated that early cultivars are best suited to drier sites (less than 350 mm) where the advantage of yield stability in lower-rainfall years outweighs their inability to fully exploit the best seasons. Acevedo (1987) listed early flowering as one of the attributes able to maximise the partitioning term of yield which, in the case of grain yield, is the harvest index of the crop. Bidinger and Witcombe (1989) added that short duration cultivars can easily be bred as the heritability of flowering time is usually high, and the character is easily assessed.

Plant height was neither particularly important in discriminating between adapted and non-adapted germplasm to drought, nor was it related to the yield response (Tables 7, 9, 11, 12, 15 and 16). It had been reported by Ceccarelli *et al.* (1987a) concerning barley and wheat, and by Hadjichristodoulou (1987) for barley, that tall lines gave higher yield than short ones in moisture-limiting conditions. However, Acevedo and Ceccarelli (1989) found that in 2-row barley genotypes one of the attributes associated with a drought resistance index was the short stature and that this trait was better expressed in the naturally adapted germplasm (the landraces). It seems controversial whether a tall plant stature is important under dryland conditions. On the one hand, from Morgan (1989) it could be inferred that drought tolerant plants - maintaining turgor pressure by osmotic adjustment and, therefore, ability to grow as extracellular water potentials decline - should be taller, apart from genetic differences in the character, than the susceptible ones. In the present study there were some entries among the best performing (e.g., '10926' and '83022') which had a relatively taller stature. On the other hand, grain yield in water-limited environments is a function of three factors (Passioura, 1977):

grain yield =

water use x water-use efficiency x harvest index.

Maximising grain yield then becomes a function of the harvest index (HI) (Richards, 1987). It is generally agreed that a high HI is a desirable and beneficial trait to improve drought resistance (Baker, 1989, chapter 16). In recent years the major improvements in grain yield have arisen not from an increased above-ground dry matter, but from an increased HI, which has been achieved largely by reducing the height of the crop (Turner *et al.*, 1989). One of the effects of dwarfing genes in wheat is to increase the partitioning of assimilates to the spike, with consequent improvement in grain yield (Morgan, 1989). As an example, Smith (1987) reported that, under the semi-arid conditions of Oklahoma (USA), the new cultivars which have replaced the older ones and doubled the yield during the last 40 years are shorter in stature than the older varieties. Acevedo and Ceccarelli (1989) stated about barley that one possible reason for the lower effect of terminal drought on the HI of 2-row barleys is their lower stature under drought and high biomass at anthesis. In the present study, entry '7331', given its good yield, low stature and relatively high 'sink' level, could be an accession with high HI. An alternative to reducing plant height for an increase of HI is the greater transfer of carbon assimilated prior to grain filling to the grain during the grain filling period (Austin *et al.*, 1980). In the Mediterranean climate yield is correlated with the dry matter accumulation by the time of ear emergence (Turner *et al.*, 1989), and HI is mainly determined by the balance between dry matter produced (and, hence, water used) before and after anthesis (Passioura, 1977). Genotypes may differ in the ability to retranslocate stored assimilates during grain filling which could be expressed as differences in HI (Morgan, 1989). Drought during grain filling, especially if accompanied by high temperature, hastens leaf senescence, reducing the duration of this period. A greater accumulation of soluble carbohydrates in stems partially buffers plants against loss of photosynthetic capacity during grain filling (Austin, 1989). That could be another reason for taller genotypes performing better under drought, as also reported by Acevedo and Naji (1991). On the other hand, Hadjichristodoulou (1987) observed in barley that under moisture stress certain genotypes can remain greener and produce better-filled grains than others. In the present study, some cases were noticed, such as entry '37565', and entries '7178' and '7419' in 1989-90, that, without "sacrificing" their earliness in heading, were able to delay somewhat the leaf senescence, thus obtaining a relatively long grain filling period.

As already mentioned, the considered environment is likely to face low temperatures during canopy development with the possibility of frost. In the present work frost tolerance appeared several times as one of the best discriminating characters between adapted and non-adapted germplasm (Tables 7, 9, 11, and 16). Freezing damage in dry environments can cause yield loss both directly *via* tiller mortality and ear sterility (Single, 1975) and indirectly *via* loss of leaf area and delayed flowering and maturity (Harris *et al.*, 1987). The severity of damage will depend on the stage of plant development. Frosts occurring at a late growth stage are a hazard of semi-arid areas. Even quite mild frosts (about < -3° C) occurring in the late elongation, booting or heading stages result in severe yield reduction with little opportunity for recover as the crop enters periods of high temperature and water deficit. Frosts occurring during early elongation can cause death of the main stem, but tillers are able to recover. However, flowering and maturity will be delayed and some yield loss might occur. Loss of leaf area in the early growth stages (before stem elongation) with screen night temperatures less than about -8° C occurs quite frequently. Reduction in canopy size through this effect is expected to lead to water-use inefficiencies, as a poor ground cover allows increased evaporative loss from bare soil surfaces which reduces the water available for crop use (Cooper, 1983). Acevedo (1987) suggested the ability to grow under suboptimal temperatures and the resistance to low temperatures as two of the attributes able to maximise transpiration as a fraction of evapotranspiration. In the two seasons of the present study, frosts affected the crop practically at any stage between tillering and booting. It is therefore difficult to understand which aspects of the damaging mechanisms were most critical and by which means the best yielding entries were, usually, also more frost tolerant. It would be essential to separate the effect of the two stresses and "quantify" how drought tolerant and how frost tolerant are the identified best materials. It might also be important to detect what is the relationship between frost tolerance and the ability to grow at low temperature. Low winter temperatures indeed restrict crop growth rates, resulting in slow development of full ground cover, with similar consequences on the water balance to those previously mentioned about frost damage.

Early growth vigour was not an important character in this study for discriminating between adapted and non-adapted germplasm. Conversely, many references in the literature support its importance by the positive correlation found between this trait and grain yield under drought (e.g., Turner and Nicolas, 1987; Richards, 1987; Turner *et al.*, 1989; Acevedo and Ceccarelli, 1989; Acevedo and Naji, 1991). According to Fisher (1979) improved growth during winter will be better from the point of view of a greater water use efficiency as well as decreasing the evaporation term of ET. However, Nachit and Ketata (1987) found that there may be an optimum vigour beyond which an excess of vegetation will not be beneficial.

The number of spikes per unit area also did not seem a relevant trait in selecting the best performing materials. There was a trend towards a positive effect of a higher number of spikes (Tables 7, 9 and 11) but this was not supported statistically. In similar environments to the one of the present analysis Hadjichristodoulou (1987) reported for barley high and stable yields of genotypes with high numbers of tillers and low variance for the character. Acevedo and Naji (1991) and Nachit (1991) found in durum wheat a high and consistent positive correlation between number of fertile tillers and grain yield under drought conditions. Conversely, several authors suggested reduced tillering as a mechanism to improve grain yield under moisture-limiting conditions (e.g., Donald, 1968; Richards, 1983a; 1987; Clarke, 1987; Austin, 1989; Simane *et al.*, 1993). A limited number of tillers is seen by all these scientists as a stress avoidance mechanism in that it conserves water for grain filling. According to Sinha (1987) the size of the 'sink' could influence the senescence of the leaves and plant: the larger the 'sink' the faster the senescence.

The number of kernels per spike could only be recorded in 1988-89, when it proved highly correlated to grain yield (Table 9). This is in agreement with several studies. Gebeyehou *et al.* (1982) reported that number of kernels per spike was the yield component most related to yield in durum wheat grown under drought conditions in Saskatchewan. Annicchiarico and Pecetti (1993) found that kernel number per spike was highly correlated with yield under Mediterranean conditions, being also a character discriminating the material capable of a high and stable yield across seasons. The same character proved to be predominantly related to grain yield under moisture stress applied at different timings during the crop cycle (Simane *et al.*, 1993). From the physiological point of view, maintenance of a positive turgor by osmotic adjustment has been advocated (Morgan, 1980, 1983) as a mechanism which maintains in turn seed set. According to Richards (1987) it is possible that a high dry matter at anthesis sets a high potential kernel number whereas osmotic adjustment buffers the crop to drought just before flowering, when kernel number is most susceptible, the result being the establishment of a large 'sink'.

Peduncle length proved a very important character, given its relationship to good performance in both seasons (Tables 9, 11, 12, 15, 16 and 17). Sinha (1987) stated that the peduncle, together with the flag leaf and the ear, contributed with its photosynthesis to assimilation after anthesis. It could perhaps be inferred from Morgan (1989) that plants which possess a high osmotic adjustment and, hence, a positive turgor, being able to maintain elongation of the shoots would have longer peduncles, as this internode elongates when the stress begins to be critical in the considered environment. Unfortunately, with the exception of the studies carried out at ICARDA, no other references could be found on the importance of this trait on yield performance under dryland conditions. The results presented by Nachit (1989, 1990, 1991), by Acevedo (1990), by Acevedo and Naji (1991), and by Nachit *et al.* (1992) showed a consistent and high positive correlation between peduncle length and grain yield, as in the present work. Peduncle length was never significantly correlated with earliness in the current study. However, groups of entries highly differing for grain yield also differed simultaneously for earliness and peduncle length (Tables 11, 15 and 16). If earliness, as previously discussed, is the main mechanism for drought escape and if peduncle length is related to mechanism(s) of drought tolerance, then the presence at the same time in well adapted materials of earliness and long peduncle could suggest a kind of combination of both escape and tolerance in those entries.

Considering the best yielding out of the whole set of materials (Table 13), the data herein presented did not suggest the identification of *an* "ideotype" able to cope with the given, harsh environment, but rather the presence of different combinations of positive traits almost at the individual level. Indeed, the "escapers" with rather long grain filling period and "economical" tillering were selected

('7419' and '10926') together with the "escapers" with relatively high number of spikes ('M13' and 'M21'). An "escaper" with relatively large 'sink' and, possibly, high harvest index was also identified ('7331'). Similar performance was obtained by the frost and, probably, drought-"tolerant" lines ('83022', '83089' and '83008'), by the "tolerant" line with rather long grain filling period and very large 'sink' ('7178'), as well as by the "tolerant" line with rather long grain filling period and relatively low number of spikes ('37565'). A dwarf type with short grain filling period ('37499') may owe its good performance to high HI through a fast retranslocation rate. Such a variability of plant structure related to a desirable yield response is in agreement with the findings of Ceccarelli *et al.* (1991) on barley and Annicchiarico and Pecetti (1993) on durum wheat genotypes evaluated in the same Mediterranean region.

These results point to the difficulty of combining different mechanisms of adaptability into a unique "ideotype". However, a careful selection of parents in breeding programmes based on the knowledge of their trait structure could allow the combination of desirable and compatible characters into new, diversified plant types. Though referring to a limited number of entries, the present findings highlight the existence of plant types which have not been exploited, and perhaps not even explored, by the breeders in this region.

Some of the most interesting genotypes identified in the present study, especially those tentatively classified as "tolerant", could be the basic materials for some follow-up activities, the main aim of which would be the identification of possible underlying physiological mechanisms by means of appropriate tools. An assessment of differences between some genotypes for the previously described mechanism of osmotic adjustment has been made in this study. The experiment will be described in section 5. It might be worth investigating other mechanisms such as carbon isotope discrimination ($\Delta^{13}C$), xylem vessel diameter, or post-anthesis translocation of assimilates from stems and leaves to the developing grain.

In glasshouse studies on wheat (Farquhar and Richards 1984; Condon *et al.* 1990; Ehdaie *et al.* 1991) and other crop species, plant water use efficiency has been shown to be negatively correlated with the value of carbon isotope discrimination, $\Delta^{13}C$, measured in dry matter, as predicted from the theory of leaf gas exchange (Farquhar *et al.* 1982; Farquhar and Richards 1984). These relationships at the whole plant level have been obtained under both well-watered conditions and when water supply was restricted. The consistent results obtained in these glasshouse studies and the observations that genotypic variation for $\Delta^{13}C$ in wheat is substantial (Condon *et al.* 1987, 1990; Ehdaie *et al.* 1991) and that $\Delta^{13}C$ has a high broad-sense heritability (Condon and Richards 1992; Ehdaie *et al.* 1991) all indicate that $\Delta^{13}C$ may prove a useful selection criterion in breeding for greater water use efficiency and hence yield in wheat. A negative relationship between $\Delta^{13}C$ and water use efficiency is, therefore, expected also under field conditions. However, in field studies with wheat, relationships between above-ground dry matter production and $\Delta^{13}C$ and/or grain yield and $\Delta^{13}C$ have often been positive (Condon *et al.* 1987; Turner *et al.* 1989; Ehdaie *et al.* 1991). Even though water use has not been measured in any of these studies, there has been little indication of a negative relationship between water use efficiency and $\Delta^{13}C$. Richards (1987), Turner *et al.* (1989) and Condon *et al.* (1993) indicated that a possible reason for the positive relationship between $\Delta^{13}C$ and yield in Mediterranean climatic regions is that lines with high $\Delta^{13}C$ grow faster and mature before severe stress develops. Condon *et al.* (1993) suggested that if the correlation between $\Delta^{13}C$ and early canopy growth can be broken, it should be possible to combine the intrinsic water use efficiency associated with low $\Delta^{13}C$ with the high efficiency obtained by having a larger leaf area during the cool, early phase of crop growth.

Increased root hydraulic resistance was first proposed by Passioura (1972) as a desirable trait for plants growing under drought. Subsequent work showed that this can be best achieved by decreasing the diameter of the main xylem vessel in the seminal roots (Richards and Passioura, 1981a, 1981b). The root resistance had primarily been considered for crops grown predominantly on stored water, but it is thought to be advantageous in a Mediterranean environment as well, preventing the plant from using water too freely during vegetative growth. Results presented by Richards (1987) confirmed that in all environments lines with small xylem vessels yielded more than lines with larger vessels. The yield advantage was greatest in the driest environments, but there was no yield penalty in having small xylem vessels in good environments. Data from Acevedo (1987) support a conservative strategy in terms of water use and a greater resistance to liquid water flow in plants of the most drought tolerant crop in northern Syria (barley landraces) as compared to other crops (improved barley and wheat). It would be interesting to assess whether durum wheat lines with different responses to water stress also differ for vessel diameter and, therefore, hydraulic resistance.

It has been mentioned that in wheat grain yield is dependent on assimilates produced by current photosynthesis in the post-anthesis period, post-anthesis carbohydrates stored temporarily in vegetative organs before being re-translocated to the grain, and assimilates translocated from stored carbohydrates in the vegetative plant parts produced during the pre-anthesis period. The contribution of pre-anthesis assimilates to final yield can be up to 30% (Bidinger *et al.* 1977). This contribution may be even higher in Mediterranean-type environments where rainfall diminishes and water becomes limiting in the post-anthesis period during grain filling (Johnson and Moss 1976; Pheloung and Siddique 1991). The ability to effectively translocate assimilates from stems and leaves to the developing grain is desirable for maximising grain yield production in water-limited environments (Turner and Begg 1981). However, in practice, year-to-year variation in water deficits makes reliable selection for the character difficult in dryland breeding programs. Blum *et al.* (1983a, 1983b) suggested that treatment of cereal plants 10 to 14 days after anthesis with a desiccant to arrest photosynthesis was a method of assessing the ability of lines to maintain growth from assimilates stored before treatment, thus assessing the ability to maintain a high harvest index under simulated water-limited conditions. The technique proposed by Blum *et al.* (1983a) was partially modified (Turner *et al.*,1989; Nicolas and Turner, 1993) concerning the plant stage of chemical treatment (one-third grain filling, rather than a fixed number of days from anthesis) and the chemical compound (potassium iodide instead of magnesium chlorate). However, Regan *et al.* (1993) have recently shown some limitations to the technique in dryland wheat improvement. In particular, where there is a final drought in the crop season or diseases cause early senescence of leaves, the desiccation treatment will not generate sufficient variation among genotypes for selection to be possible.

3 *Field assessment of durum wheat performance in eastern Sicily: Libertinia 1990-1993.*

3.1 *Introduction*

Libertinia is a location representative of the durum wheat growing zones in the hilly, inner part of Sicily, as described in section 1.1.2. It lies in the eastern part of the island (37°30' N, 14°35' E, 150 m asl), about 45 km west of the city of Catania and the coast (see Figure 2). The soil is a clay-loam, containing 49% sand, 18.5% silt and 32.5% clay. Total nitrogen is lower than 0.1% (Kjeldahl method), which is considered poor. The organic matter content (1.28%) and the P_2O_5 concentration (17 ppm) are also low, but the K_2O concentration is relatively good (197 ppm). The pH is sub-alkaline: 7.98 in the top 20 cm layer.

Compared to the climatic conditions described for northern Syria (section 2.1), those of Libertinia can be considered more favourable. However, relative to the rest of Italy this location is characterised by rather stressful conditions. The following information on the climate of Libertinia has been extrapolated from 30-year data (1921-1950) recorded at 163 meteorological stations in Sicily (Anonymous, 1971). Libertinia has an average annual rainfall (September to August) of about 600 mm, 80% of which is concentrated between October and March (the wettest months being generally November, December and January). In this period water surpluses occur (water lost with run-off and, after soil saturation, deep drainage) because rainfall exceeds the evapotranspiration. Therefore, the effective available water for crops during that period is about 300 mm. A water deficit becomes evident from May onwards, estimated at about 17 mm for May and 72 mm for June. Unlike northern Syria, some showers do occur during July, August and September, due to summer storms, but these have little influence on winter cereals such as wheat. The temperature regime does not have the low winter minima which are typical of northern Syria. Libertinia is affected by the influence of the temperate coastal climate, whereas Breda has a marked continental-type Mediterranean climate. The lowest monthly average mean daily temperature occurs in January and February with 8.5° C. Frost events are exceptional in this location. Maximum daily temperature above 30° C are common in June and may also occur in the second half of May as a consequence of the 'Scirocco' wind.

3.2 *Methods*

In June 1990 an individual, representative plant was collected from each of the 75 entries included in the previously described experiment Breda 1989-90 (section 2.1.1). Given the cleistogamous pollination of wheat, these plants can be practically considered as pure lines. The 75 lines so isolated were then grown at Libertinia during the three seasons between 1990-91 and 1992-93. Dealing with pure lines must have reduced the genetic buffer of a possibly heterogeneous population structure such as that of landraces (Ceccarelli *et al.*, 1991), but must also have reduced undesirable experimental variability caused by the possible presence of different genotypes in the tested entries, as the genetic status of accessions in germplasm collections is seldom known (Pecetti *et al.*, 1992b).

The rainfall and temperature patterns of the three evaluation seasons are shown in Figure 7. The seasonal rainfall (October-June) in 1990-91 was 378 mm. Its distribution was quite good until April, then the amount was low in May and June. However, there were little signs of drought stress. That was also due to the

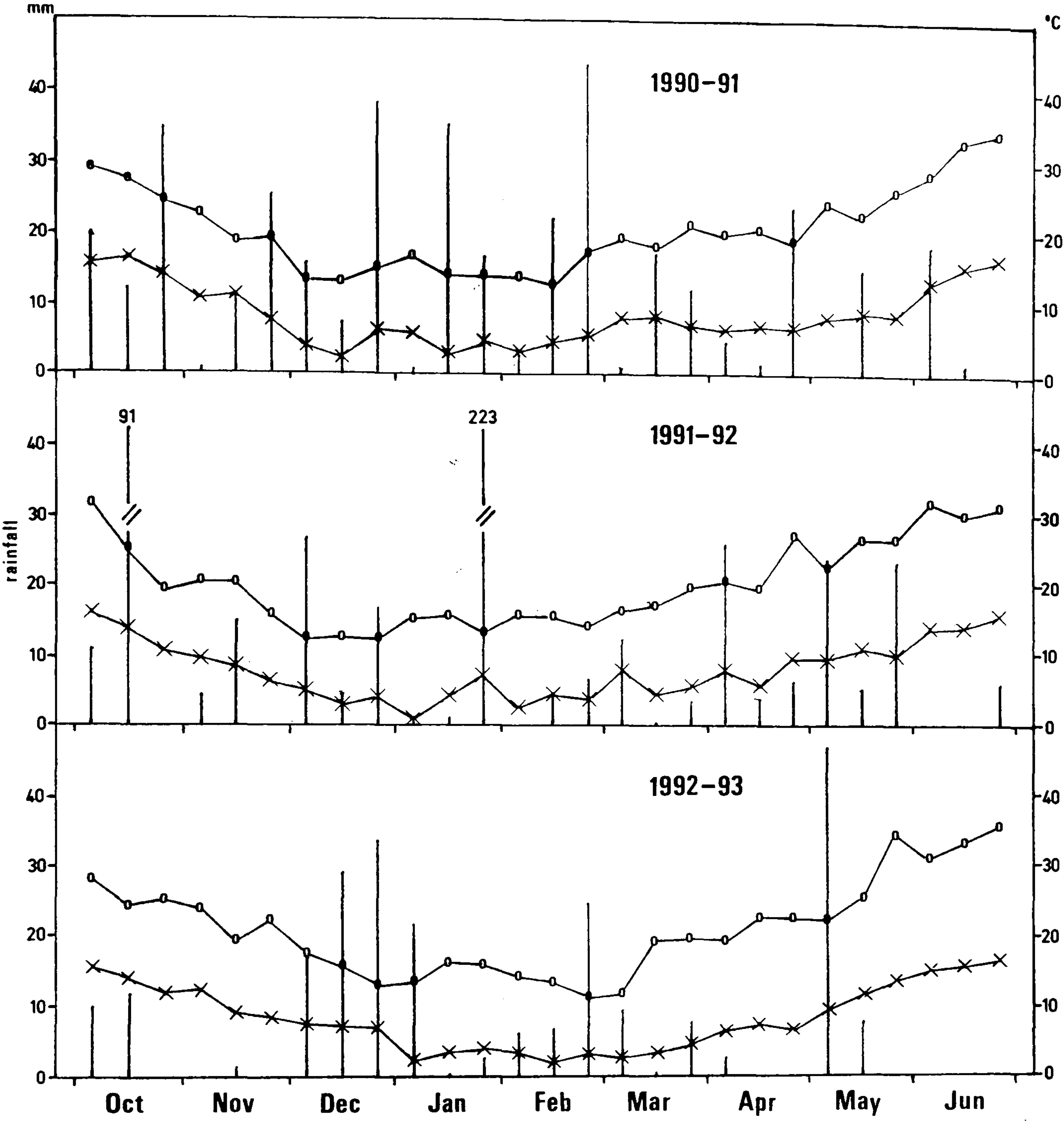


Figure 7. Ten-day rainfall (|), average daily maximum (—o—) and minimum (—×—) temperature in 1990-91, 1991-92 and 1992-93 at Libertinia, eastern Sicily.

fact that high temperatures (> 30° C) were not present during the grain filling period.

Rainfall during the season 1991-92 reached 511 mm, 38% more than in the previous season, mainly due to an exceptionally wet January (> 200 mm). In contrast, February and March were dry but this did not seem to affect the crops, probably because of sufficient soil moisture reserves. A sharp increase in maximum temperature occurred in the second half of April, but no heat stress was encountered in May or June.

The season 1992-93 was characterised by rainfall of 268 mm between October and June. The distribution was quite favourable for crops until the second half of April, when a severe dry spell occurred. The high rainfall in the first ten days of May probably did not completely compensate for this lack of moisture, and the season overall must be regarded as rather unfavourable. Maximum temperatures showed a steep increase in the second half of May, which hastened the physiological maturity of the crop.

In 1990-91 the 75 pure lines were sown as single-head-progenies in rows of 30 spaced seeds (at 4.5 cm) derived from the individual plants collected at Breda. Row spacing was 17 cm. As no replications could be made due to the limited seed available, the rows were laid out according to the modified augmented design (Lin and Poushinsky, 1983) so that an adjustment of the observed values and a comparison between entries could be made on the basis of the performance of replicated control cultivars. In order to improve the efficiency of adjustment, data of characters not recorded on a plot basis were taken on ten plants per row and the averaged value used for the adjustment allowed by the design. 'Simeto', 'Duilio', 'Capeiti' and 'Russello' were used as control cultivars, i.e., two modern, improved varieties, one old cultivar and one local landrace, respectively. Due to rain, sowing was delayed to the 20th of December, about three weeks later than usual. The fertilizer rate was 36 kg ha^{-1} of N and 92 kg ha^{-1} of P_2O_5 prior to sowing and 32 kg ha^{-1} of N in each of two applications during winter (end of January and end of February).

In 1991-92 the 75 genotypes were sown in a randomised complete block design with three replications. 'Russello', 'Capeiti' and 'Simeto' were again used for reference. The improved cultivar 'Duilio' was replaced as control in 1991-92 by the recently released variety 'Vespro'. Each entry in each replication was a plot of three rows, 1.5 m long and 17 cm apart. Sowing took place at the end of November at a rate of about 400 seeds m^{-2}. Fertilizer rate was the same as in 1990-91.

In the season 1992-93 the experiment was carried out exactly as in 1991-92 in terms of plot size, experimental design, sowing rate and date, and fertilizer rate. 'Simeto', 'Capeiti', 'Arcangelo' and 'Vespro' were the reference cultivars added to the 75 entries.

At a juvenile stage (at about emergence of the sixth leaf) the following characters were recorded in each season:

- *early growth vigour*, scored on a plot basis using the same 5-level scale adopted at Breda for this character (section 2.2) from very poor to very good;
- *total leaf area*, measured on each of ten plants taken at random from the row (excluding the two end plants) in 1990-91, from the plot in the two following seasons;
- *shoot fresh weight*, measured immediately after harvesting on ten random plants from the row (in 1990-91) or from the plot (in the two following seasons);
- *shoot dry weight*, measured after oven drying the same ten plants at 105° C for 24 hrs.

Later on, *heading date* and *maturity date* were recorded as number of days from January 1st to, respectively, 50% heading and 50% physiological maturity in the row or in the plot. On each of ten random plants per row or per plot the following traits were further recorded:

- *plant height*;

- *peduncle length*;
- *number of spikes per plant*;
- *number of spikelets per spike*;
- *number of kernels per spike*;
- *1000-kernel weight*;
- *grain weight per spike*;
- *awn length*, measured at maturity on a single awn from a spikelet in the middle of the spike;
- *awn weight*, measured on the same awn;
- *awn weight per unit length*, calculated by dividing the weight of the awn by its length;
- *grain yield per plant*. Although in 1991-92 and in 1992-93 the plots were sown at normal density, the grain production was also expressed as yield per plant, for consistency between the three seasons. Obviously, the competition caused by plant density was different in the first season relative to the other two.

As can be seen, the durum wheat evaluation in Sicily focused mainly on the same aspects that were examined in the experiments carried out in Syria, with two differences. The first one was a greater emphasis given to the measurements of early growth. This was chosen to verify the relationship between an early vigour and grain yield. Besides the visual score already adopted in Syria to record this character, the methodology proposed by Turner and Nicolas (1987) was used, which includes the measurement of the plant weight at about the 6-leaf stage. The total plant leaf area was further recorded in the present study to give an estimation of plant vigour at that stage.

The second difference between the evaluation in Sicily and that in Syria was the inclusion of measurements regarding the awns: their length, weight and weight per unit length (an estimation of their thickness). These traits were recorded to assess their importance in a Mediterranean environment. Awns are generally believed to increase yields under moisture-limiting conditions (Evans *et al.*, 1972; Hadjichristodoulou, 1987; Ali Dib *et al.*, 1990). The advantage conferred by the awns is due to their ability to contribute substantially to ear photosynthesis, even when the rest of the plant is dry (Grundbacher, 1963; Evans and Dunstone, 1970; Evans *et al.*, 1972). Selection for possession of awns in wheat has been acknowledged as a beneficial trait to improve drought resistance, especially in the presence of terminal drought (Richards, 1982; Baker, 1989, chapter 16). In the case of durum wheat the majority of lines do possess long awns. The question would be whether there is still variability for the length, surface area and thickness of the awns among genotypes differing for many other traits, and whether this variability, if present, could account for at least some differences in the yield performance.

In 1990-91 the observed data were adjusted prior to further statistical analyses on the basis of the recorded values of the control plots, according to the adopted experimental design (Lin and Poushinsky, 1983). In the two other seasons, the recorded data were used for all statistical analyses. The best performing entries, not differing from the top-yielding one, were identified in each season. Entry separation was according to the computed LSD for the modified augmented design (Lin and Poushinsky, 1983) in 1990-91, according to Duncan's test in 1991-92 and 1992-93. To evidence the characteristics which contributed to their better adaptation, the group of top lines was compared by t-test with the remaining entries for all recorded traits. Correlation coefficients between grain yield per plant and the other traits were calculated for the whole set of lines in each season.

In order to verify in other environments the efficacy of selection based on the visual score, as adopted in Syria for drought resistance assessment (section 1.2.1), the two groups of 25 selected (according to the score) and 50 non-selected (randomly taken) entries which constituted together the full set of 75 lines (section 2.2) were also compared by t-test for all characters in each season.

3.3 *Results*

Overall mean values for the recorded traits in the three seasons are shown in Table 19. The 75 entries proved to be a diverse set of germplasm, as already noted in Syria (see Table 10). Wide phenotypic variation existed for all traits. For instance, there were both dwarf entries as short as the improved control cultivar and very tall lines. It is worth mentioning that the two shortest entries in the three seasons were not improved varieties but Moroccan landraces ('M13' and 'M21'). Their average plant height across seasons was respectively 66% and 72% of the average height of the whole 75 lines, and 88% and 97% of the average height of the modern, dwarf cultivar 'Simeto'.

There were between-season differences in all characters except days to heading (data not shown). The separation of seasonal mean values is shown in Table 19. The overall mean yield in 1991-92 was similar to that in 1990-91 (both seasons appeared favourable to the crop). Some differences existed for other traits between the 1990-91 and 1991-92 seasons. These could be generally ascribed to the fact that in the latter season the plants were grown at a greater density than in the former, when they were spaced. That explains, for instance, the lower plant weight and leaf area at the juvenile stage, as well as the lower kernel number and weight recorded in 1991-92. It is possible that the plant density also explains the lower awn weight in the second season, while awn length seemed much less influenced. However, an effect of the severe lodging due to high rainfall in 1991-92 cannot be excluded on those characters recorded at maturity. Despite the dense conditions of growth, in 1991-92 plants produced more fertile tillers than in 1990-91, thus compensating for the reduction of the other yield components.

The data from 1992-93 highlight the effect of the most stressful season of

Table 19. Overall mean values of 75 durum wheat entries for the characters recorded in three seasons at Libertinia.

	1990-91	1991-92	1992-93
Character	Mean (± s.e.)	Mean (± s.e.)	Mean (± s.e.)
Early growth vigour (scale 1-9)	7.3 ± 0.2 A	6.8 ± 0.1 B	6.7 ± 0.1 B
Leaf area/plant[a] (cm^2)	16.6 ± 0.8 A	9.6 ± 0.3 B	8.2 ± 0.2 C
Fresh weight/plant[a] (mg)	693.4 ± 30.3 A	447.5 ± 9.2 B	490.2 ± 15.0 B
Dry weight/plant[a] (mg)	129.5 ± 15.7 A	73.0 ± 1.7 B	115.1 ± 6.2 A
Heading date (dd. from Jan 1)	125.3 ± 0.7 A	124.3 ± 0.6 A	125.9 ± 0.3 A
Maturity date (dd. from Jan 1)	165.5 ± 0.4 A	165.0 ± 0.2 A	157.1 ± 0.2 B
Plant height (cm)	109.5 ± 2.0 A	105.1 ± 1.6 A	69.9 ± 1.3 B
Peduncle length (cm)	40.3 ± 0.9 A	41.8 ± 0.6 A	23.0 ± 0.7 B
No. spikes/plant	6.2 ± 0.2 B	7.9 ± 0.2 A	7.9 ± 0.2 A
No. spikelets/spike	22.8 ± 0.3 A	20.2 ± 0.3 B	14.2 ± 0.2 C
No. kernels/spike	52.7 ± 1.6 A	48.7 ± 0.9 B	28.5 ± 0.7 C
1000-kernel weight (g)	47.9 ± 0.9 A	38.3 ± 0.9 B	35.4 ± 0.6 C
Grain weight/spike (g)	2.55± 0.10 A	1.81± 0.04 B	1.03± 0.03 C
Awn length (cm)	13.7 ± 0.3 A	13.0 ± 0.2 A	10.7 ± 0.2 B
Awn weight (mg)	401.2 ± 20.5 A	215.1 ± 8.9 B	197.6 ± 6.2 B
Awn weight/unit length ($mg\ cm^{-1}$)	29.3 ± 1.3 A	16.2 ± 0.5 B	18.1 ± 0.4 B
Grain yield/plant (g)	10.43± 0.64 A	10.39± 0.28 A	5.66± 0.24 B

[a] at a juvenile stage.

Seasonal mean values for each character followed by the same letter are not different at $P \leq 0.05$, according to Duncan's test.

evaluation on some characters. Indeed, grain yield per plant was much lower than in both 1990-91 and 1991-92. At the same time, a drastic reduction relative to the two previous seasons occurred for plant height (and peduncle length), kernel number and weight, number of fertile spikelets per spike and awn length. The number of fertile tillers per plant did not seem adversely affected by the growing conditions in 1992-93, probably in compensation for a lower plant density at heading, due to the less favourable conditions. The growth cycle was shorter, with an earlier date of maturity. As already mentioned, this was due to a terminal heat stress which occurred in 1992-93 (see Figure 7). In general, when the evaluation was carried out with dense sowing (seasons 1991-92 and 1992-93), the variability of the genotype values was smaller than that recorded when the plants were spaced (season 1990-91), as indicated by the standard error of means (Table 19).

The analysis of grain yield per plant separated 11 entries (not differing from each other) as the best yielding in 1990-91 (Table 20). Their average yield was 18.7 g per plant, with individual values ranging between 16.3 and 23.6 g per plant, all superior to the overall mean value of 10.4 g per plant of the whole set of lines. The good adaptation of the 11 top entries is also shown by the fact that their yield values were never lower than those of the improved check varieties (13.4 g for 'Simeto', 13.8 g for 'Duilio'), while the best yielding accession, namely the Jordanian landrace '83089', was significantly superior to both these cultivars. '83089' is the accession already noted for its good performance in two seasons at Breda (section 2.3), and was used in the experiment described in section 5 where it showed the capability to adjust its osmotic potential under drought stress at an early stage of ontogeny.

In 1991-92, entry differences for grain yield per plant were significant ($P \leq 0.01$) but entry mean separation was not as clear-cut. Duncan's test separated 36 entries as the best yielding not differing from each other and from the top one (Table 20). The average yield of this group of top lines was 12.2 g per plant, ranging between 10.3 and 16.6 g per plant. These extreme values were comparable with those of the control varieties which ranged between 10.1 g per plant of 'Russello' and 14.5 g per plant of 'Vespro'. None of the best lines differed significantly from any of the four checks according to Dunnett's test which is used for comparison of means with a control (Dunnett, 1964). The four lines which had a greater yield than the best control cultivar 'Vespro' (although not significantly) were two landraces from Turkey ('6614' and '7788') and two landraces from Tunisia ('6834' and '9705').

In 1992-93, entry differences for grain yield per plant were significant ($P \leq 0.001$), and Duncan's test identified 20 entries as the top yielding (Table 20). The average yield of this group was 8.5 g per plant, with a minimum of 6.7 and a maximum of 11.2 g per plant. The control cultivars had mean yields ranging between 6.6 g per plant of 'Simeto' and 9.0 g per plant of 'Capeiti'. None of the top yielding entries differed significantly from the control cultivars. The first six ranking accessions, which had a greater yield than 'Capeiti' (although not significantly different), were '83063' from Jordan, '7833' from Turkey, '83005' from Jordan '37499' from Greece, '4727' from Ethiopia and '12257' from the former USSR. Entry '37499' also appeared among the best yielding accessions at Breda in 1988-89 and 1989-90 (see Tables 6 and 13). This genotype seems therefore promising for breeding purposes under severe stress conditions.

The group of top yielding entries in each season was compared with the group of remaining entries for all characters. Table 21 reports the traits for which the group mean values differed significantly ($P \leq 0.05$) in each season (according to the t-test). The best yielding lines obviously outyielded significantly the remaining ones, and this superiority was accompanied by higher values for the three yield components number of spikes per plant, number of kernels per spike and 1000-kernel weight. As the combination of the latter two traits, grain weight per spike was also higher in the top than in the other group in each season. Apart

Table 21. Comparison of character mean values between the group of best yielding entries (Top) and the group of the remaining entries (Rest) in each season. Number of top entries was: 11 in 1990-91, 36 in 1991-92, and 20 in 1992-93.

	1990-91			1991-92			1992-93		
Character	Top		Rest	Top		Rest	Top		Rest
Fresh weight/plant^{a} (mg)	865.9	*	660.8		-			-	
Heading date (dd. from Jan 1)		-			-		123.6	***	126.8
Peduncle length (cm)	44.6	*	39.3		-			-	
No. spikes/plant	8.9	***	5.7	8.2	*	7.5	9.4	***	7.3
No. spikelets/spike		-			-		16.1	***	13.5
No. kernels/spike	59.9	*	51.1	51.6	***	45.7	34.6	***	26.2
1000-kernel weight (g)	54.7	***	46.5	40.1	*	36.2	39.2	***	34.0
Grain weight/spike (g)	3.24	**	2.41	2.00	***	1.62	1.37	***	0.91
Awn weight (mg)		-		233.4	*	195.8		-	
Awn weight/unit length (mg cm^{-1})		-		17.3	*	15.2		-	
Grain yield/plant (g)	18.72	***	8.86	12.25	***	8.42	8.46	***	4.63

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[a] at a juvenile stage.

*, **, *** : group means in each season different at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively, according to t-test.

from the yield components, the two groups differed for other traits, specifically in each season. In 1990-91 the top entries showed higher mean values than the others for fresh weight per plant at the juvenile stage and for peduncle length. It is worth noting that the difference in the length of the last internode was not related to any difference in the total height of the plant, as the two groups had, on average, an almost identical stature (108.6 cm for the top group, 109.6 cm for the other). In 1991-92, the best yielding lines possessed heavier awns, both as absolute weight and weight per unit length. In 1992-93 the top group was also characterised by a higher number of fertile spikelets per spike and by earlier heading (the maturity date also tended to be earlier, though this was not statistically significant).

Correlation analysis of grain yield per plant with the other characters largely confirmed the relative importance of the various features contributing to good performance in each season (Table 22). Grain yield per plant was correlated in all three seasons with the three yield components, and with grain weight per spike. Other significant correlations, although of a much lower magnitude, were shown in 1990-91 with the parameters of juvenile growth (viz., early growth vigour, fresh weight and dry weight per plant and total leaf area), peduncle length, number of fertile spikelets and awn weight. Awn weight, both absolute and relative, was also positively correlated with grain yield in the season 1991-92. In that season all the significant correlations were lower than in the two other seasons. In 1992-93, the correlation analysis highlighted the relevance of earliness in conferring good performance in a poor year (Table 22). The fact that shorter genotypes tended to yield better is more difficult to explain. A possibly lower incidence of lodging damage on the shorter types should be excluded as a reason for the yield advantage, as in 1992-93 no lodging was observed due to the low total rainfall. The high correlation between plant height and peduncle length ($r=0.90$, $P\leq0.001$) explains the negative trend between length of this internode and grain yield. In that, the

Table 22. Correlation coefficients (r) between grain yield per plant and other characters in each season of evaluation at Libertinia. Only significant ($P \leq 0.05$) coefficients are reported.

Character	1990-91	1991-92	1992-93
	Correlation coefficients with grain yield per plant[a]		
No. spikes/plant	0.80 ***	0.45 ***	0.66 ***
Grain weight/spike	0.72 ***	0.61 ***	0.84 ***
No. kernels/spike	0.61 ***	0.35 **	0.78 ***
1000-kernel weight	0.61 ***	0.32 **	0.59 ***
Awn weight/unit length	0.41 ***	0.33 **	-
Fresh weight/plant[b]	0.39 ***	-	-
Awn weight	0.36 **	0.29 *	-
Early growth vigour	0.31 **	-	-
Dry weight/plant[b]	0.29 *	-	-
Peduncle length	0.29 *	-	-0.24 *
Leaf area/plant[b]	0.25 *	-	-
No. spikelets/spike	0.24 *	-	0.71 ***
Heading date	-	-	-0.68 ***
Plant height	-	-	-0.37 **
Maturity date	-	-	-0.25 *

[a] number of observations is 75 for all correlations.

[b] at a juvenile stage.

*, **, *** : significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

results differ from those of Breda where the peduncle tended to be longer in the best yielding entries irrespective of their total stem height. It is worth noting that in the two seasons with lowest rainfall (1990-91 and 1992-93) the absolute awn weight and weight per unit length were positively correlated with the grain weight per spike and the number of kernels per spike. Only in 1992-93 were these weights also correlated with the kernel weight.

The seasonal lists of top yielding entries reported in Table 20 show that 49 entries out of 75, that is, two thirds of the whole set, appeared at least once in the group of the best performing lines. It is evident from the table that the genotypic response was largely season-specific. That was confirmed by the genotype x season interaction analysis which was allowed by the replicated trials carried out in 1991-92 and 1992-93. This interaction for grain yield per plant was significant at a probability level of 2% (data not shown). Nonetheless, there were entries included in the top yielding group in more than one season. Eight of the 11 best yielding entries in 1990-91 (Table 20) were also included among the best 36 in 1991-92. These lines were therefore highly responsive to favourable growing conditions, such as those experienced in 1990-91 and 1991-92.

Of the 20 entries belonging to the best yielding group in 1992-93, 10 were also present in the group of 36 top yielding entries in 1991-92. Given the different climatic conditions encountered in 1991-92 and in 1992-93, for these 10 entries a good adaptation to a range of environments can be postulated. Five entries were present in the top yielding group in all three seasons. These were '4727' from Ethiopia, '83089' from Jordan, '83008' from Jordan, '37565' from Greece, and '83005' from Jordan. In order to examine their morpho-physiological characteristics across seasons in comparison with the whole collection of 75 entries, the mean values of each variable in each season (reported in Table 19) were set to 100 and the individual values for the five entries indexed accordingly. Table 23 shows the average indexed values across the three seasons for each character of

Table 23. Average across three seasons (1990-91 through 1992-93) of the indexed values for the recorded characters (mean of the whole set of 75 entries = 100) of the five durum wheat entries out of 75, which were among the best yielding ones in all three seasons.

	Best yielding entries				
Character	4727	83089	83008	37565	83005
Grain yield/plant	132	177	156	131	155
Heading date	93	97	96	94	97
Maturity date	98	100	99	99	99
Plant height	89	98	101	85	93
Leaf area/plant[a]	113	74	100	98	115
Fresh weight/plant[a]	128	85	114	88	143
Dry weight/plant[a]	108	73	99	80	129
No. spikes/plant	119	124	114	108	124
Peduncle length	101	105	102	98	99
No. spikelets/spike	101	108	101	95	102
No. kernels/spike	122	124	121	114	104
Grain weight/spike	109	148	131	117	117
Awn length	63	105	93	93	109
Awn weight	48	107	103	83	96
Awn weight/unit length	68	102	115	90	92
1000-kernel weight	92	119	112	103	113

[a] at a juvenile stage.

the five above-mentioned genotypes. Their constant yield superiority relative to the whole set of entries is evident, the average indexed values ranging between 131 and 177. Compared to the mean yield of the two control cultivars used commonly in the three seasons (the traditional variety 'Capeiti' and the modern variety 'Simeto'), the average indexed yields across seasons of the five genotypes were as follows: 104 for '4727', 139 for '83089', 123 for '83008', 105 for '37565', and 118 for '83005' (100 being the mean seasonal yield of 'Capeiti' and 'Simeto'). Interestingly, this yield superiority was not accompanied by a unique combination of the other morpho-physiological features. There was, however, a certain common earliness of heading, more marked in '4727' and '37565'. None of the five lines was appreciably different in maturity date from the whole set of materials. The three genotypes from Jordan did not seem to possess dwarfing genes, which is expected as all of them are native landraces and do not derive from recent breeding activities. The relatively shorter stature of '4727' from Ethiopia is in accordance with the generalised feature of the Ethiopian germplasm (Pecetti *et al.*, 1992a). The dwarfness of '37565' may be a clue to a possible introgression of modern germplasm into this Greek genotype. The number of kernels per spike was the yield component consistently associated to a high and stable yield, its indexed values ranging between 104 and 124. In most cases, a high kernel number per spike seemed due more to high intra-spikelet fertility than to high number of fertile spikelets per spike, which was, nonetheless, always above the average.

The number of kernels per spikelet was not recorded but it was estimated for each plot by dividing the number of kernels per spike by the number of fertile spikelets per spike. The indexed values calculated for the five entries indicated the importance of the number of kernels per spikelet in determining a high number of kernels per spike. These values were 123 for '4727', 116 for '83089', 119 for '83008', 121 for '37565', and 102 for '83005'. The latter entry was the one with the lowest indexed value for number of kernels per spike. The other two yield components, number of spikes per plant and 1000-kernel weight, were also important in most cases in determining a high and stable yield, although entry '4727' represented an exception for the importance of kernel weight. Growth ability during winter, expressed as the plant weight or the green area per plant at the fifth/sixth-leaf stage, differed within this group of five genotypes. Entries '4727' and '83005' showed good early growth, while the indexed values of '83089' and '37565' were rather low. The awns of the three entries from Jordan were generally longer and/or heavier than the average, while '4727' and '37565' (especially the former) were characterised by short and thin awns.

It was very rewarding to find that all five top entries in three seasons at Libertinia belonged to the group of selected materials on the basis of the visual evaluation of drought tolerance carried out in Syria (section 1.2.1 in this thesis; Annicchiarico and Pecetti, 1990; Pecetti and Annicchiarico, 1991). That is, five out of 25 selected entries at Breda not only confirmed their adaptation to the stressful conditions at Libertinia in 1992-93, but had also a good performance in the two more favourable seasons 1990-91 and 1991-92.

When the groups of selected and non-selected entries on the basis of drought tolerance score used in Syria were compared for their behaviour at Libertinia, they were significantly ($P \leq 0.05$) different in the three seasons for the characters reported in Table 24. In 1990-91 and, particularly, in 1992-93 the selected entries showed a yield superiority over the other materials. The fact that the selected group was earlier in heading than the non-selected one is not likely to account for the yield advantage shown in 1990-91, as earliness was not significantly correlated with grain yield per plant in that season (see Table 22). In contrast, the higher 1000-kernel weight of the selected group certainly contributed to its better performance. In 1992-93 the discrimination among accessions made in Syria appeared also very effective in Sicily. Indeed, the two groups differed widely

Table 24. Comparison of character mean values between the group of 25 selected (S) entries and the group of 50 non-selected (NS) entries on the basis of their agronomic score at Breda, evaluated in three seasons at Libertinia.

	1990-91			1991-92			1992-93		
Character	S		NS	S		NS	S		NS
Heading date (dd. from Jan 1)	121.1	***	127.2	121.2	***	125.8	124.0	***	126.9
Plant height (cm)		-		99.3	*	108.0	64.6	**	72.5
Peduncle length (cm)		-			-		21.1	*	24.1
No. spikelets/spike		-		19.2	**	20.6	15.7	***	13.5
No. kernels/spike		-			-		33.2	***	26.1
1000-kernel weight (g)	52.1	**	46.2		-		38.5	***	33.8
Grain weight/spike (g)	2.86	*	2.43		-		1.30	***	0.90
Grain yield/plant (g)	12.15	*	9.68		-		7.43	***	4.77

*, **, *** : group means in each season different at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively, according to t-test.

in terms of grain yield per plant, and such a difference was accompanied by the difference in heading, already noted in 1990-91 and 1991-92, as well as in kernel number and weight which accounted for the difference in grain weight per spike. Also the number of spikes per plant tended to be higher in the selected group than in the non-selected one (8.3 versus 7.6), the difference being significant at a probability level of 6%, i.e., just above the threshold of 5%. As in 1991-92, the selected entries were also shorter than the non-selected ones, and this probably contributed to the slight negative correlation between plant height and grain yield observed in 1992-93 (Table 22). The consistency of earliness in heading of the selected group was not surprising, as early heading was one of the main criteria in the attribution of the score in Syria (Annicchiarico and Pecetti, 1990). The character was evidently stable across very different environments of evaluation.

3.4 *Discussion*

The selection criteria most useful at Libertinia do not appear fully consistent with those at Breda, at least in the seasons considered in this evaluation. At Breda, earliness in heading and, partly, in maturity (i.e., stress escape) was of paramount importance for good performance. Some relevance could also be attributed to possible mechanisms of stress tolerance, assuming that peduncle length is an indicator of such tolerance (Nachit and Jarrah, 1986). In contrast, at Libertinia the yield potential *per se*, resulting from the three yield components, appeared very important. Only in the most unfavourable season at Libertinia (1992-93) was there a positive effect associated with early heading. The advantage conferred by an earlier heading date might be attributed to the need to escape the stressful conditions encountered during this season. The possible selection for a long peduncle presented some uncertainty at Libertinia, because its relationship with high yield was not as clear-cut as in Syria.

In 1990-91 and 1991-92 there was a positive relationship between awn weight (both absolute and relative) and grain yield. In 1992-93 such a correlation was not present. Attributing a role in drought tolerance to the awns (Evans *et al.*, 1972; Richards, 1982; Hadjichristodoulou, 1987; Ali Dib *et al.*, 1990), it seems that in 1992-93 (the most stressed of the three seasons of evaluation) the mechanism(s) of stress escape (not important in the first two relatively favourable seasons) prevailed over the mechanism(s) of stress tolerance. Awn length was never correlated with grain yield. This observation suggests that the awn parameters contributing to a better performance were their area and/or thickness. It is likely that this contribution to higher yields may also be indirect, through a positive effect on spike fertility and, to some extent, kernel size. This is indicated by the positive correlations existing in some cases between awn weight (both absolute and relative) and these yield components. These correlations suggest either a possible role of heavy (=wide and thick) awns on determining positive spike attributes, or a linkage between awn size (excluding the length), spike fertility and kernel size.

In 1990-91 there appeared to be a relationship between the plant weight (of the aerial part) at an early stage of development and the final grain yield per plant, in line with the findings of Turner and Nicolas (1987). However, the features of the five top lines across seasons (Table 23) suggest once again (see also section 2.3) that a good and stable performance under Mediterranean conditions is not necessarily associated with an above-average early growth.

Plant height appeared negatively correlated with grain yield in the less favourable season (1992-93), despite its claimed importance as a selection criterion in moisture-limiting environments (Ceccarelli *et al.*, 1987a). The controversial role of this trait under drought has already been discussed in section 2.4. It must be underlined that as regards the present set of accessions a trend for the best performing entries to be shorter statured than others has already been shown under severe stress conditions (see Table 7). A genetic relationship (in a broad sense, i.e., linkage or pleiotropic effects), specific for these materials, between good adaptation to this conditions and short stature cannot be excluded.

The lower correlations observed in 1991-92 than in the two other seasons between grain yield and the correlated traits (Table 22) suggest a smaller influence of these traits on higher yields in that season which was characterised by unusual rainfall. Other characters than those recorded might account for the genotype performance under these conditions. Among them are likely to be lower susceptibility to lodging and to pathogens (in particular mildew and rusts).

Confirming what has already been observed at Breda, the results from Libertinia showed that high and stable yields can be attained by genotypes possessing different morphological architectures (Annicchiarico and Pecetti, 1993; section 2.3 in this thesis). However, as already shown in Syria (Annicchiarico and Pecetti, 1993), in Sicily earliness of heading and high spike fertility contributed to good performance across different environmental conditions (Table 23).

The results showed that durum wheat landraces could be a reservoir of adapted materials for the Sicilian environment. In particular, the Jordanian gene pool was confirmed to be a source of valuable germplasm under Mediterranean conditions (Pecetti and Annicchiarico, 1991). If one of the aims of the breeding activities in Sicily is to broaden the genetic base of the varieties presently available (Boggini *et al.*, 1990, 1992), the five genotypes here identified as the best yielding across seasons could certainly be suitable for the purpose. They could possibly introgress variability into existing genetic backgrounds without deteriorating their positive features for productivity.

As regards the possibility of utilising useful genes from novel sources, it would be worth investigating the nature of the dwarfism in the two Moroccan landraces ('M13' and 'M21') which were the shortest-statured entries consistently in all three seasons. This finding reinforced previous results showing that the Moroccan durum wheat gene pool includes sources of dwarfism (Benlaghlid and Monneveux, 1989; Pecetti and Nachit, 1993). Although it is not possible to trace back their exact site of origin, these two accessions were collected in 1984 during a mission in southern Morocco organized for collecting landraces of durum and bread wheat (Perrino *et al.*, 1986). If real landraces (that is, if no introduction of foreign germplasm had occurred in the sites of origin prior to the collecting mission), these two entries might bear dwarfing genes different from those deriving from 'Norin 10' and their identification would be of great genetic interest.

Selection for grain yield proved to be rather environment (=season)-specific, due to the occurrence of a strong genotype x season interaction. Nonetheless, it was possible to identify some lines which were able to perform well in more than one season. It was also possible to find some genotypes which seemed adapted to both the stressful conditions of Breda and the relatively favourable conditions of Libertinia. To some extent, the selection made in Syria also seemed effective for the Sicilian locality. That is not surprising, as it has been shown for barley (Ceccarelli and Grando, 1991) and durum wheat (Pecetti *et al.*, 1992b) that some of the material selected under unfavourable conditions is able to retain its superiority in a more favourable environment. For barley, the proportion was about 20% of the selected genotypes, and for durum wheat about 30%. In both cases, such a proportion was higher (8-fold for barley, 7-fold for durum wheat) than the proportion of lines selected under favourable conditions which were also able to perform well in a stressful environment. In the present study, five out of the 25 selected genotypes at Breda gave high and stable yield at Libertinia. This proportion (20%) seems in line with those previously reported.

It was interesting to see how the visual assessment of performance especially devised for the Syrian environment became a more effective means of selection in Sicily under lower rainfall. The less climatically favourable were the growing conditions, the more the distinction between selected and non-selected entries resembled that between top yielding genotypes and the rest of the collection (see Tables 21 and 24). In particular, the mean yield of the selected group was 103% that of the non-selected group in 1991-92 (511 mm rainfall), 125% in 1990-91 (378 mm rainfall), and 156% in 1992-93 (268 mm rainfall).

4 *Simulation modelling*

4.1 *Introduction — The CERES-Wheat model*

The International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT) project has produced a computer software package called the Decision Support System for Agrotechnology Transfer (DSSAT). The current version of DSSAT contains models for several crops. The Crop Estimation through Resource and Environment Synthesis (CERES)-Wheat model is the DSSAT model for wheat. The following information on the model was derived from Ritchie (1984), Jones *et al.* (1984), Godwin *et al.* (1984), and Godwin *et al.* (1989). CERES-Wheat is a yield model developed for several purposes such as assistance with farm decision making, risk analysis for strategic planning, within-year management decisions, policy analysis, etc. It simulates the effects of weather, soil water and genotype on crop growth and yield. CERES-Wheat has the main features needed for a user-oriented model. That is, it requires a minimum of readily available soil and weather data; it is written in a familiar computer language; and it is computationally efficient requiring only seconds for a simulation run. It has a daily time-step and variation of several factors occurring almost minute-by-minute is integrated into daily functions through empiricisms which have been developed (Ritchie, 1984).

Phasic development, or the duration of the various growth phases, is considered a very influential factor in determining final yields, and is therefore given great importance in the model. The crop phenology components of CERES-Wheat describe the changing allocation of dry matter accumulation among plant organs during the course of crop growth. The growth stages used in the model and the growth of organs in each stage are listed in Table 25. In the model, phenological development is driven by the accumulation of daily thermal time (DTT), that is, the difference between daily mean air temperature and a base temperature of 0° C. If the mean temperature is below 0° C, DTT is 0, while it is reduced due to high-temperature stress if the mean temperature is above a critical "optimum" temperature of 29° C. Photoperiod and vernalisation requirements are also taken into account by the model to simulate phenological development. Daylengths shorter than 20 hrs. slow the development of the crop during stage 1. The shorter the daylength, the slower that phenological development occurs at a given temperature. A genotype-specific coefficient for photoperiod is available in CERES-Wheat, where it is coded as P1D. The coefficient P1D, as well as the other genotype-specific coefficients described later, range from zero or one to an uppermost value corresponding to the maximum known expression of the trait. For instance, P1D ranges from 1 to 5. These user-expressed "scale" values are converted to "biological" values within the model. These biological values indicate the relative amount that development is slowed when plants are grown in a photoperiod 1 hr. shorter than the optimum, which is assumed to be 20 hrs. (Godwin *et al.*, 1989). The coefficient of vernalisation (P1V) represents the relative amount that development is slowed for each day of unfulfilled vernalisation, assuming 50 days is sufficient for all varieties. Another developmental phase which is genotype-dependent is the linear grain fill (stage 5). The grain filling duration coefficient (P5) indicates the degree days above a base of 1° C from 20° C days after anthesis to maturity.

CERES-Wheat computes dry-matter production, leaf growth and root growth which are then corrected by reduction factors for non-optimal temperatures (below 18° C for photosynthesis and 21° C for leaf growth) or for suboptimal soil water availability. The number of grains per unit area is determined by the stem weight at the end of pre-anthesis ear growth and by further genotype-specific coefficients. G3 is the spike number coefficient, expressing the dry weight of a

Table 25. Growth stages used in the CERES-Wheat model and plant parts growing during each stage (in parentheses). From: Ritchie (1991).

Stage	
7	Presowing
8	Sowing to germination
9	Germination to emergence (roots, coleoptile)
1	Emergence to terminal spikelet initiation (roots, leaves)
2	Terminal spikelet initiation to end of vegetative growth and beginning of ear growth (roots, leaves, stems)
3	End of vegetative growth and beginning of ear growth to end of pre-anthesis ear growth (roots, leaves, ear)
4	End of pre-anthesis ear growth to beginning of linear grain filling (roots, stems)
5	Linear grain filling (roots, stems, grain)
6	End of grain filling to harvest

single stem (excluding leaf blades and sheaths) and spike, under no stress, when elongation ceases. G1 is the kernel number coefficient, the kernel number per unit weight of stem plus spike at anthesis. The maximum growth rate of grains during stage 5 is determined by the genotype-specific coefficient G2 which defines the kernel filling rate under optimum conditions. This rate is also limited by temperature and by the amount of carbohydrate available for grain growth.

The six above-mentioned genotypic coefficients are provided with the model for many bread wheat cultivars but for only a few durum cultivars. When a new variety is used in a simulation, the first step is to match the cultivar with those that have already been described in the model. If this is not possible, approximate values of the coefficients for a genotype for which experimental data are available can be obtained by trial and error (Godwin *et al.*, 1989). Once a satisfactory goodness-of-fit between predicted and observed phenological and yield data is obtained, the coefficients can be applied without further calibration in other experiments.

The soil water balance is calculated in CERES-Wheat to evaluate the possible yield reduction caused by soil and plant water deficits. Three key levels of water availability for each soil layer are required as input: i) saturation moisture content, ii) drained upper limit, or field capacity and iii) lower limit, or wilting point. If field values are not available, the model uses several laboratory-measured soil physical and chemical parameters as input for estimating the potentially extractable soil water from each layer. Infiltration of water into the soil is calculated as the difference between precipitation (or irrigation) and run-off. Run-off curves (USDA SCS, 1972) are user-specified by numbers varying between 60 and 100. Run-off is then calculated from these curve numbers according to soil type and slope. Whole profile drainage rate coefficients are input as a number reflecting the rate of drainage from the most impeded soil layer in the profile. Evaporation calculations reduce the climatic data requirements to daily values of precipitation, minimum temperature, maximum temperature and solar radiation. Soil surface albedo, obtained from a scale of surface colours, and soil texture are also required inputs in the evaporation calculations. By estimating root growth and distribution components, the model calculates a maximum water uptake for each soil layer when water availability is known. The ratio between water supply and demand in the profile is termed 'soil water deficit factor' and is used by the model to modify the rate of photosynthesis, tillering, leaf expansion, senescence, and the distribution of assimilates.

Besides climate and soil data, the following management parameters are required inputs for the model: sowing date, plant population (plants m^{-2}) or seed rate, row spacing, and sowing depth.

CERES-Wheat also includes a nitrogen component, describing the nitrogen cycle between soil and crop. That was, however, considered beyond the scope of crop modelling use in the present study and was not used.

CERES-Wheat model has been validated for a large number of diverse wheat-growing environments, including those with limited water availability (Otter and Ritchie, 1984; Harris and Godwin, 1989; Moulin and Beckie, 1993). The model has proved to be "portable", that is, to operate for any cultivar, location, season and management system that is capable of being fully specified in terms of model input data (Thornton *et al.*, 1991).

4.2 *Methods*

The CERES-Wheat crop-growth model, version 2.10, was used to simulate the performance of durum wheat genotypes at Breda (northern Syria, 35°56' N, 37°10' E, 300 m asl) and Libertinia (eastern Sicily, 37°30' N, 14°35' E, 150 m asl). Historical weather data were available for 12 seasons (1980-81 through 1991-92) at Breda, and six seasons (1987-88 through 1992-93) at Libertinia. Daily values of precipitation, minimum temperature, maximum temperature and solar radiation were recorded at Breda, while for Libertinia solar radiation was not directly recorded but was estimated from the other recorded variables according to Bindi and Miglietta (1991). Average monthly values of rainfall and total seasonal (October to June) rainfall for each season in the two locations are shown in Figures 8 and 9. It is worth noting that for Breda the rainfall between October and June represents the whole annual precipitation while at Libertinia there is a further average amount of about 70 mm between July and September, mostly due to summer storms. Total seasonal rainfall at Libertinia (398 mm, on average) is greater than at Breda (262 mm) and this is so throughout the season with the possible exception of February (average monthly data not shown). Figures 8 and 9 indicate that not only is the total seasonal amount of rain variable among seasons, but also that the distribution within seasons varies from year to year. At Breda, the wettest season (1987-88) was followed by the two driest ones (1988-89 and 1989-90). Similarly, at Libertinia the wettest season (1991-92) was followed by the driest (1992-93). In both localities dry spells occurred in various periods within different seasons. For instance, at Breda early drought in autumn was present in 1980-81 and 1985-86; low precipitation in December and February was a feature of both 1983-84 and 1990-91. The season 1988-89 was characterised by no rain after December, except for two showers in March and May which probably saved the crop from complete failure, which occurred in 1989-90 when the situation was also aggravated by late frosts. Rainfall in May, which is very important as it occurs during grain filling and ripening, varied greatly among seasons. It was satisfactory or good in 1980-81, 1981-82, 1982-83, 1990-91 and 1991-92 (in the latter season after no rain in April), but was scarce or absent in 1983-84, 1984-85, 1986-87 and 1989-90 (Figure 8). Also the incidence of low temperatures was

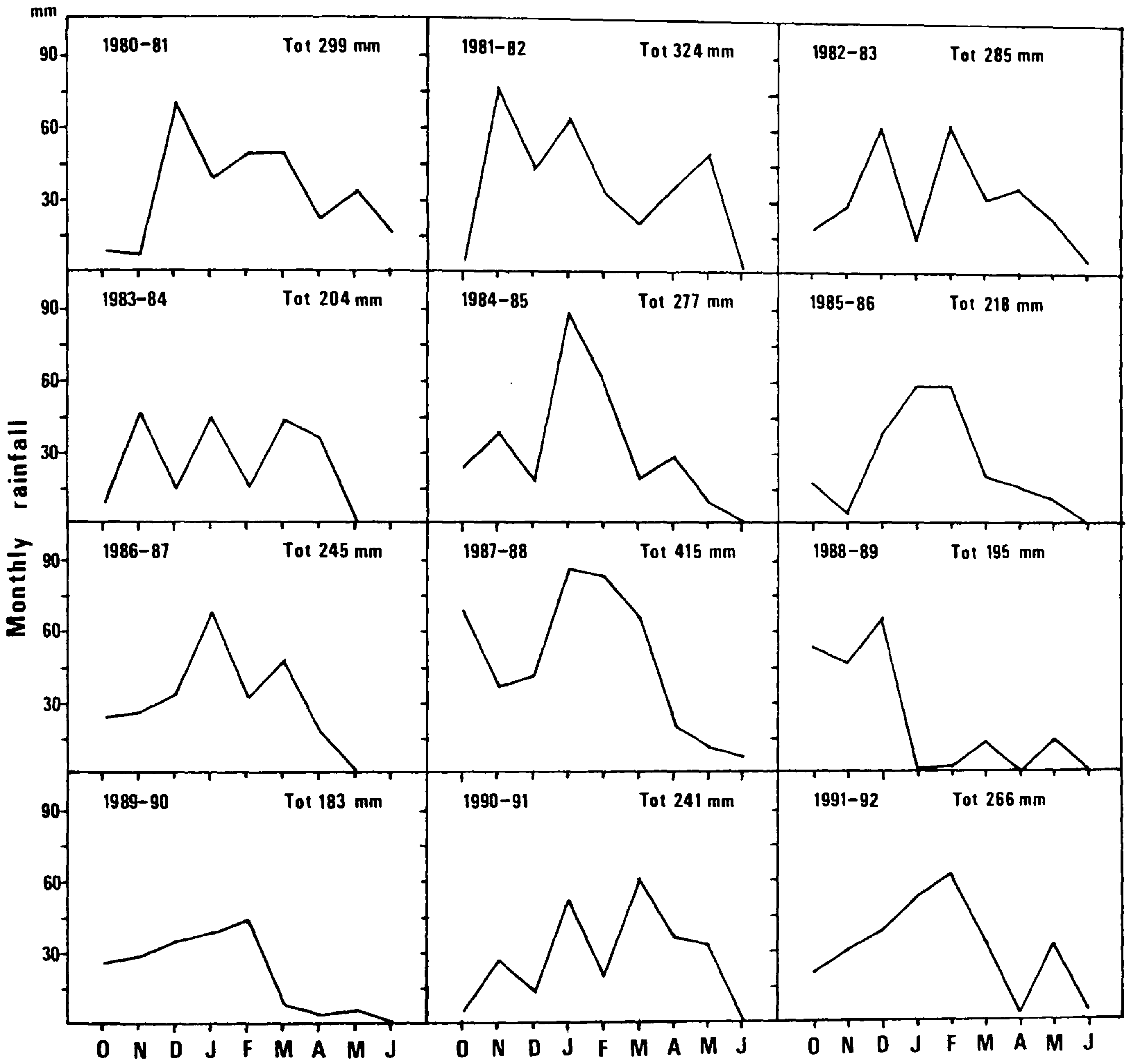

Figure 8. Recorded monthly rainfall in 12 seasons of simulated crop growth at Breda, northern Syria.

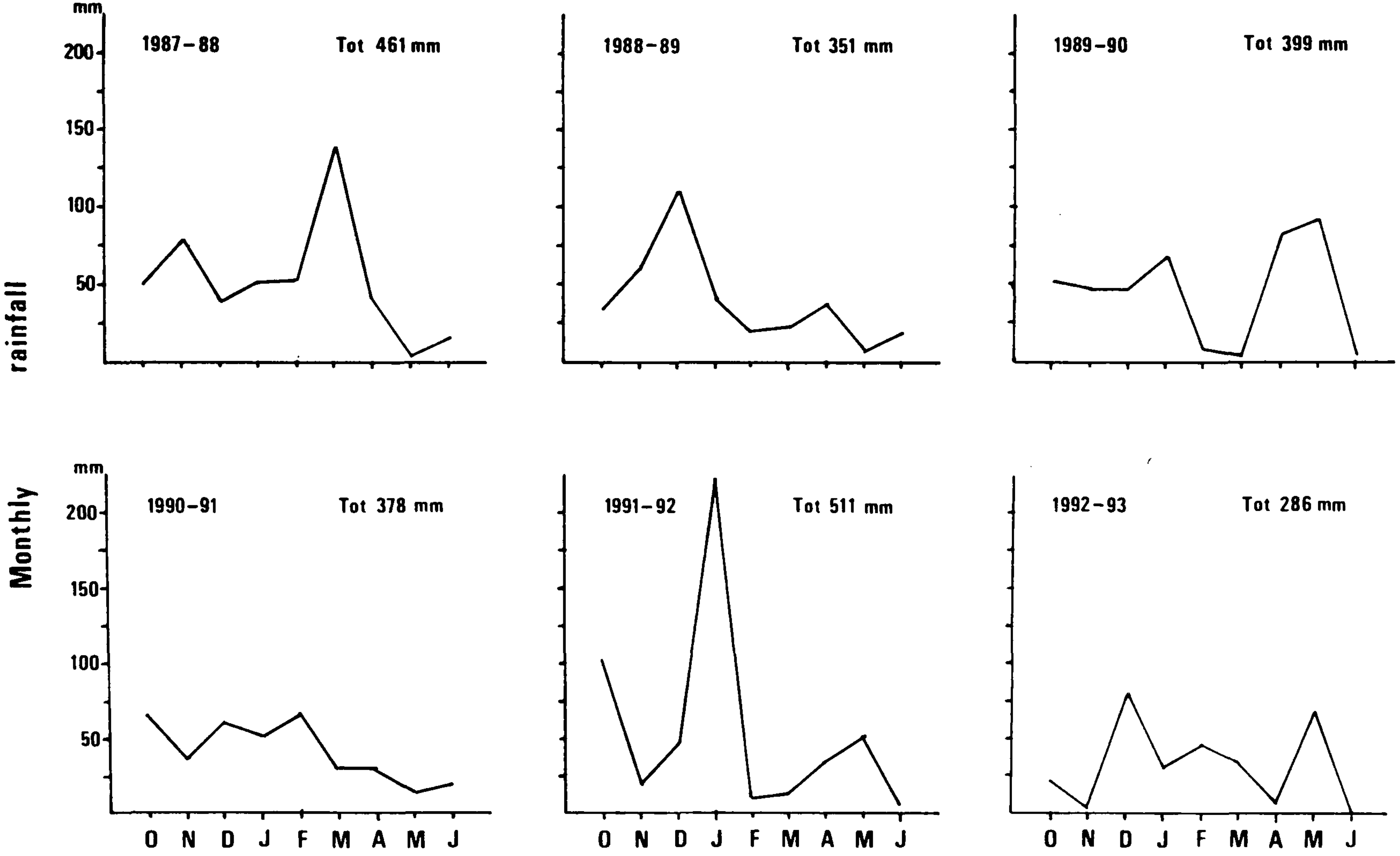

Figure 9. Recorded monthly rainfall in six seasons of simulated crop growth at Libertinia, eastern Sicily.

very variable among seasons (data not shown). The season 1982-83 was colder than average throughout. Cold winters occurred in 1984-85, 1986-87, 1988-89 and 1989-90. Late frosts of particular severity were experienced in 1981-82, 1982-83, 1984-85, 1986-87 and 1989-90.

As regards Libertinia (Figure 9), drought in April-May occurred in 1987-88, 1988-89 and 1990-91. The season 1989-90 had an odd rainfall distribution, being very dry in February and March and receiving slightly less than half of its total rainfall during April and May when rains are expected to decline in Mediterranean environments. The season 1991-92 was very dry in February-March, in spite of the highest recorded total rainfall due to an exceptionally wet January. The season 1992-93, rather dry until April, received a large proportion of precipitation in May, which probably rescued those cereal crops which were not too early.

The soil parameters which were input for the simulation runs of both localities are reported in Table 26. Besides these, other required parameters were estimated by the CERES-Wheat model, using soil texture, bulk density and soil organic matter information provided for each locality. The estimated soil variables were the lower limit of soil water availability (wilting point), the drained upper limit of soil water availability (field capacity), and the saturation moisture content.

The simulation examined two genotypes ('83022' from Jordan and '10926' from France) characterised by a good real performance under severe drought (section 2.3, Table 6), and by satisfactory behaviour under more favourable conditions (data not shown). In field trials, '10926' proved distinctly earlier in heading and maturity than '83022' (about five days, on average, in Syria). The characteristics of '83022' suggested a possible drought tolerance for this landrace, while '10926' seemed to possess a certain ability to escape the most severe stress (section 2.3). It should be emphasised that '83022' is a landrace very similar to 'Haurani', the widespread and well adapted Syrian landrace, and therefore it is likely as adapted to the stressful conditions prevailing in the environment of

Table 26. Soil parameters input for the two localities of crop simulation with the CERES-Wheat model.

For the whole profile	For each layer
Soil surface albedo	Moist bulk density
First-stage evaporation coefficient	pH
Whole profile drainage rate coefficient	Coarse fraction (> 2 mm) %
Runoff curve number	Clay fraction (< 0.02 mm) %
Initial soil water index	Silt fraction (0.02-0.05 mm) %
Number of layers in the profile	Sand fraction (> 0.05 mm) %
Thickness of soil layers	Organic carbon %

evaluation.

None of the cultivars already input in the CERES-Wheat model seemed to posses genetic coefficients which would give reliable predictions for the two genotypes. Therefore, observed values from two contrasting environments (Breda 1988-89 and Libertinia 1991-92) were used to approach by trial and error the coefficients that gave the most realistic estimation of phenology and production for both genotypes in both localities. Those coefficients were subsequently used in all simulation runs. As suggested by Harris and Godwin (1989) for durum wheat genotypes, the phyllochron interval (PHINT), or the thermal time for the appearance of a leaf, which drives crop physiological development, was reduced at Breda from the default value of 95 degree days. For '83022' 85 degree days, and for '10926' 80 degree days gave the best goodness-of-fit with the observed data.

Crop management simulated in the two localities was the standard for each of them. At Breda row spacing was 30 cm, sowing depth was 4 cm and density was 150 plants m^{-2}. At Libertinia the corresponding values were 17 cm, 5 cm and 300 plants m^{-2}. The difference between practices at the two sites simply reflects the generally different climatic conditions under which the crop is grown. As regards plant density, it is well established that in the presence of favourable conditions, higher density gives better yields than a lower one (Stapper and Harris, 1989). Experimental evidence confirms that the plant populations adopted in the present study can be considered optimal for the two environments to maximise the respective grain production (Stapper and Harris, 1989; Mariani and Novaro, 1993).

Cropping after fallow was simulated in the two sites with no application of irrigation.

Three sowing dates were simulated at both localities. Sowings in the second half of November are typical for winter cereals in the Mediterranean area and 26 November was assumed as "normal" sowing date. That was, for instance, more or less the date of sowing of all the trials carried out in Syria and described in Pecetti *et al.* (1992a), Pecetti and Annicchiarico (1993) and Annicchiarico and Pecetti (1993). It is also a common period of sowing in Sicily (G. Boggini, pers. comm.). An earlier sowing date of 1 November ("early" sowing) was used to assess the reliability of the yield advantage conferred by early planting (see section 2.1), given the rather high probability of an early drought spell, and meaningfully comparing the crop phenology with the risk of late frosts (which is not taken account of by the simulation analysis). A "late" sowing date of 20 December was also simulated, as excessive rain during the second half of November and the first half of December may cause a substantial delay in sowing at both localities. The effects of such delay were therefore assessed by the simulation.

For each combination of location, sowing date and genotype the parameters reported in Table 27 were simulated.

Correlation coefficients between simulated grain yield and rainfall (total seasonal rainfall, rain between emergence and maturity, rain during growth stages 4 and 5) were computed. In addition, correlations between simulated grain yield and the water stress factor at various growth stages were analysed. Partial correlation coefficients between the simulated number of days from sowing to emergence and the simulated Julian date of anthesis, and between the simulated Julian date of anthesis and grain yield, were calculated. These coefficients were computed for equal amounts of rainfall each season, so as to remove the effects of different quantities of rainfall. The partial correlation coefficient is useful in measuring the degree of dependance between two variables after adjusting for the linear effect of one or more of the other variables. Formulae exist for computing partial correlations directly from the population simple correlations. In general, for any three variables denoted by *i,j,* and *k,* if the simple correlation for *i* and *j* is denoted by ϱ_{ij}, for *i* and *k* by ϱ_{ik}, and for *j* and *k* by ϱ_{jk}, then the partial correlation of *i* and *j* given *k* is derived as:

Table 27. Simulated parameters by the CERS-Wheat crop model for each combination of location, sowing date and genotype.

- Germination date.

- Emergence date.

- Anthesis date.

- Maturity date.

- Grain filling period (days between anthesis and maturity).

- Rainfall between emergence and maturity.

- Water stress factor affecting leaf expansion and growth at four stages:
  i) terminal spikelet initiation - end of vegetative growth and beginning of ear growth (stage 2 in Table 25);
  ii) end of vegetative growth and beginning of ear growth - end of pre-anthesis ear growth (stage 3);
  iii) end of pre-anthesis ear growth - beginning of grain filling (stage 4);
  iv) linear grain filling (stage 5).

- Average water stress factor across the various growth stages.

- Rainfall during the above-mentioned growth stages 4 and 5.

- Grain yield.

$$\varrho_{ij,k} = \frac{\varrho_{ij} - \varrho_{ik}\,\varrho_{jk}}{\sqrt{(1-\varrho^2_{ik})\,(1-\varrho^2_{jk})}}$$

(Afifi and Clark, 1984).

As already mentioned, '83022' is likely to be a stress-tolerant genotype, not particularly furnished with escape mechanisms. In order to assess which changes were induced in a "good" genetic background by modification of its development and phenology, two "dummy" cultivars were derived from '83022' by altering some of its genetic coefficients. The first new cultivar, coded as 'New1', was derived by slightly reducing the genetic coefficient relating to photoperiod (P1D), in order to shorten the vegetative growth period and bring forward the time of anthesis; all other conditions were kept as before. The second "dummy" cultivar ('New2') was derived by increasing the genetic coefficient relating to grain filling duration (P5), in order to lengthen the period between anthesis and maturity and to verify the relationship already hypothesised by Harris (1991) between grain yield and this period. The "creation" of such new cultivars was, obviously, a rough simplification of the reality, because any modifications in the development and phenology are likely to affect yield components as well. However, alteration of phenology has already been used as a simulation technique (e.g., Harris (1991)) to assess the response of a new crop's ideotype. The present model was, therefore, run using '83022', 'New1' and 'New2' with a "normal" sowing date at both localities.

The final aspect investigated by the simulation analysis was the effect of changing the initial soil water conditions. At both sites, in most cases rainfall of about 20 mm or greater occurred during the month of October (Figures 8 and 9). Therefore, at sowing (for any simulated date) water had started to replenish the soil profile after the dry summers. In all the simulation runs an intermediate initial soil water content was then simulated. An initial soil water index 0-1 is available in the programme, with 0 = all layers at the lower limit, and 1 = all layers at the drained upper limit at sowing. The routinely adopted index was 0.5, which, given the respective soil characteristics, corresponded to an average water content across the profile at sowing of 27.1% of soil (v/v) at Breda and 26.3% at Libertinia. In order to assess the effect of a sowing made on a wetter soil (e.g, after a period of good precipitation, or immediately after a shower), for the date of 26 November the simulation was also run adopting an initial soil water index of 0.7, corresponding to an average water content across the profile at sowing of 29.7% of soil (v/v) at Breda, and 28.7% at Libertinia. That is, simulated soil water content at sowing was increased by about 9% at both localities.

4.3 *Results and discussion*

Time sequences of simulated yields (Figure 10) show that for both '10926' and '83022' yields in both environments were very variable, and that this variability was not affected by the date of sowing. The median yield (exceeded in 50% of years) decreased with delayed sowing at both sites, though more markedly at Libertinia. The yield potential at Libertinia seemed greater than that at Breda as was expected on the basis of the more favourable climatic conditions encountered there. Strictly speaking, the performance at the two sites should not be compared only in terms of climatic features, since soil characteristics and crop management also differed. However, in most cases such differences were not relevant. The only remarkable exception was plant density, which was double at Libertinia compared to Breda. Therefore, just to make a "comparison" between the two environments more realistic, a simulation was run for Libertinia, using the same population density adopted for Breda (150 plants m^{-2}). The results (not reported) confirmed that

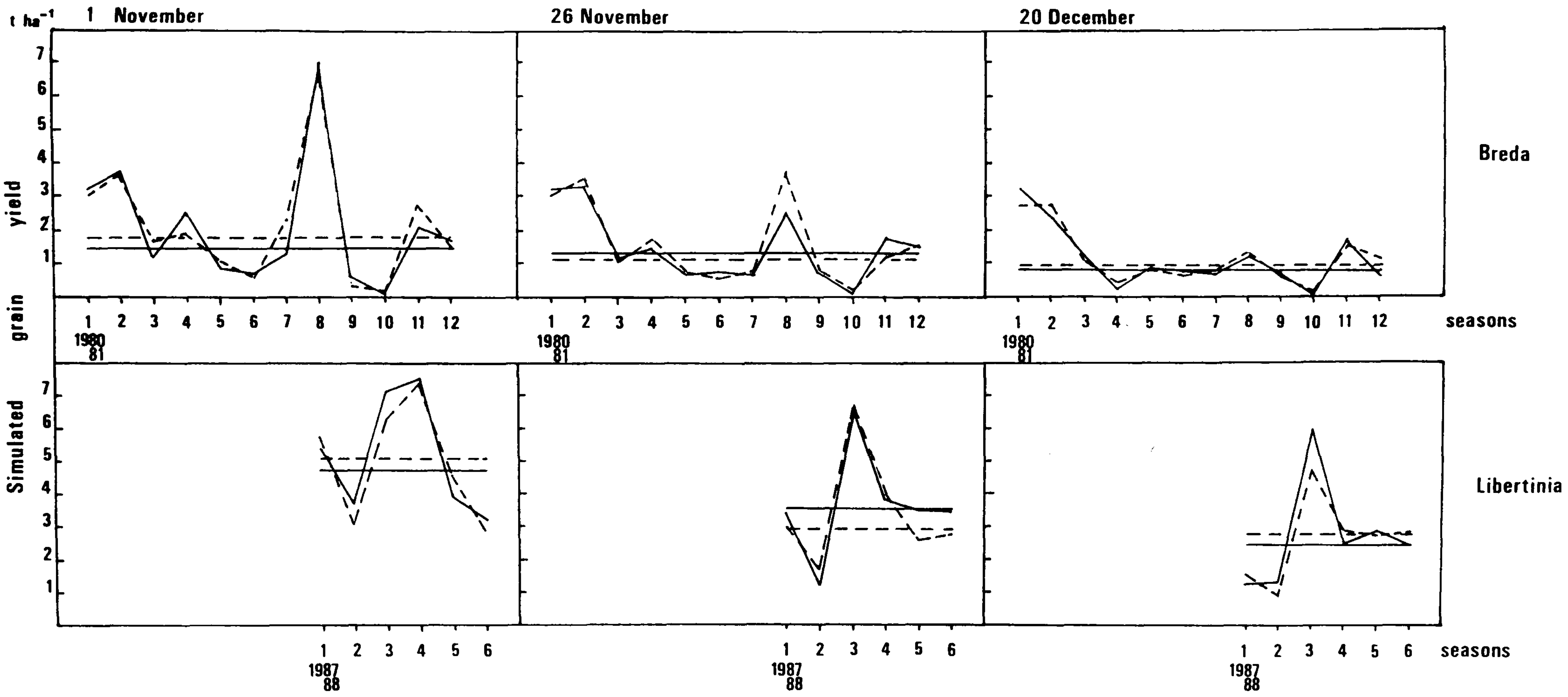

Figure 10. Simulated grain yield of the durum wheat cultivars '83022' (———) and '10926' (– – –) for three sowing dates during 12 seasons at Breda, northern Syria, and six seasons at Libertinia, eastern Sicily. The horizontal lines represent the median yields.

average yields at Libertinia with a density of 150 plants m^{-2}, though reduced relative to those with 300 plants m^{-2}, were still higher than those simulated for Breda with 150 plants m^{-2}. It is therefore likely that the large differences observed for the simulated yields in the two environments could be mainly attributed to climatic differences.

It was possible to compare the simulated yields with actually observed yields for the two genotypes in two seasons at each location: 1988-89 and 1989-90 at Breda, 1990-91 and 1991-92 at Libertinia (Table 28). In three cases out of four, the average difference for the two cultivars between simulated and observed yield was within 15% of the observed values. The result was encouraging, because this correspondence between predicted and observed yield was well within the limits of reliability calculated in the validation of this model (Otter and Ritchie, 1984; Moulin and Beckie, 1993) and of a similar model (Stapper and Harris, 1989). The only exception to this trend was the season 1989-90 at Breda, for which the model simulated very low yields, practically corresponding to a crop failure, and lower than the actually recorded yields in that season for the two genotypes. It should be emphasised that 1989-90 was the worst season since ICARDA's inception and that complete failure was experienced by many genotypes, due to the severe spring drought exacerbated by hard late frosts in the second half of March. It seems, therefore, that the model has simulated the response in that season of an "average" genotype, whereas both '83022' and '10926' were able to maintain an actual grain yield much higher than the average, probably due to mechanism(s) of frost tolerance (or escape) which the model was not able to account for. At least, the actual ranking of the seasons was respected by the model. Indeed, the season 1989-90 had the lowest yield both according to the simulation and according to the actually recorded values.

As regards the yields in other seasons for which a direct comparison was not possible, the simulated values seemed quite acceptable on the basis of repor-

Table 28. Comparison between predicted grain yield by the CERES-Wheat model and observed values for two genotypes in two seasons at each location of evaluation.

Location	Season	Genotype	Predicted ($kg\ ha^{-1}$)	Observed ($kg\ ha^{-1}$)	Difference (P - O)
Breda	1988-89	83022	739	940	- 21%
		10926	805	855	- 6%
		Mean	772	897	- 14%
	1989-90	83022	69	533	- 87%
		10926	96	670	- 86%
		Mean	82	601	- 86%
Libertinia	1990-91	83022	3789	3807	- 1%
		10926	4002	3442	+ 16%
		Mean	3895	3642	+ 7%
	1991-92	83022	3522	3896	- 10%
		10926	2588	3055	- 15%
		Mean	3055	3475	- 12%

The observed data from Breda are based on personal records; those from Libertinia were provided by Dr. M.A. Doust.

ted results of durum wheat trials at both sites, with the exception of yields greater than 6 t ha^{-1} which were predicted in certain cases. It is very unlikely that durum wheat can attain such levels of yield in those environments even under very favourable conditions. Under such conditions, the crop is very subject to constraints such as diseases and, particularly, lodging which might drastically limit the productivity, and which are not accounted for by the simulation programme. Moreover, in the present analysis, the nitrogen balance was not taken into account, and nitrogen was considered a non-limiting factor. That simplification may certainly be true under conditions of low rainfall and limited yield response. When the rainfall is abundant and the climatic conditions are favourable to the set of a large crop 'sink', nitrate leaching on the one hand, and increased nitrogen demand on the other hand, may cause this nutrient becoming a limiting factor, thereby reducing actual yields in comparison with the simulated ones.

Simulated yields for the season 1989-90 at Libertinia were probably much higher than real yields recorded in that season (a direct comparison between observed and simulated yields is not possible). Field data relative to very early genotypes (about 15-20 days earlier than those used in the present simulation) showed yields of about 1 t ha^{-1} (G. Boggini, pers. comm.). It is likely that very early genotypes were heavily penalised by the severe drought in February-March, while the simulated cultivars might have been able to recover to some extent and give higher yields making use of the good rainfall in April, during ear growth and grain filling. However, the water stress factor (scale 0-100) for stage 2 seemed rather underestimated in that season. It was 37 for '83022' and 16 for '10926' with the "normal" sowing, and zero for both genotypes with the "early" sowing. Considering the limited amount of water received during that stage of intense vegetative growth, these values seem too low, particularly for the "early" sowing date. For this reason, the very good yields in 1989-90 at Libertinia should be viewed with caution. It could then be argued that the CERES-Wheat model applied to durum wheat under Mediterranean conditions needs further calibration or modification for extreme climatic conditions. The largest differences between simulated and actual yields occurred in the case of both highest (Libertinia 1989-90) and lowest (Breda 1989-90) simulated yields.

Mean yields for each combination of location, sowing date and genotype are shown in Table 29. Confirming the findings of Stapper and Harris (1989) the simulation showed a similar trend at both sites and for both cultivars of higher yields for earlier sowing dates. "Early" sowing had the highest simulated yield (about 40% greater than "normal"), and "late" sowing the lowest (about 25% less than "normal"). Sowings during the first week of November maximise grain yields, as they allow maximum utilization of intercepted solar radiation and water when the break of season occurs early. Early crop growth costs very little in terms of water usage. Early canopy development is important, as soil evaporation losses from a bare soil during winter are almost the same as evapotranspiration from a cropped area (Stapper and Harris, 1989). Delayed sowings do not conserve soil moisture for use later in the season and, therefore, result in lower yields in good seasons. On average (across seasons and genotypes), "early" sowing at both sites experienced the highest rainfall between emergence and maturity, and the highest rainfall during the final stages of growth. At Breda, these amounts of rainfall were reduced by about 9% with "normal" sowing, and by about 26% with "late" sowing. The reductions were even higher at Libertinia (about 16% and 31%, respectively). An "early" sowing did not have a yield advantage in the lowest-yielding seasons. In these very dry seasons all three sowing dates are severely water-stressed during most of the crop cycle, so little is gained by an early development of the crop.

The change in yield with delay in sowing after 1 November varied greatly among seasons. These reductions reached values of 90 kg ha^{-1} day^{-1} delay in emergence of '83022' at Breda and 92 kg ha^{-1} day^{-1} delay in emergence at Liberti-

Table 29. Mean (± std. error) across seasons of simulated yield (kg ha^{-1}) of two durum wheat cultivars at two locations for three sowing dates.

Location	Cultivar	Sowing date		
		1 November	26 November	20 December
Breda	83022	2051 ± 543	1485 ± 301	1121 ± 261
	10926	2114 ± 517	1560 ± 343	1162 ± 240
Libertinia	83022	5136 ± 745	3649 ± 685	2746 ± 712
	10926	4973 ± 748	3466 ± 719	2601 ± 534

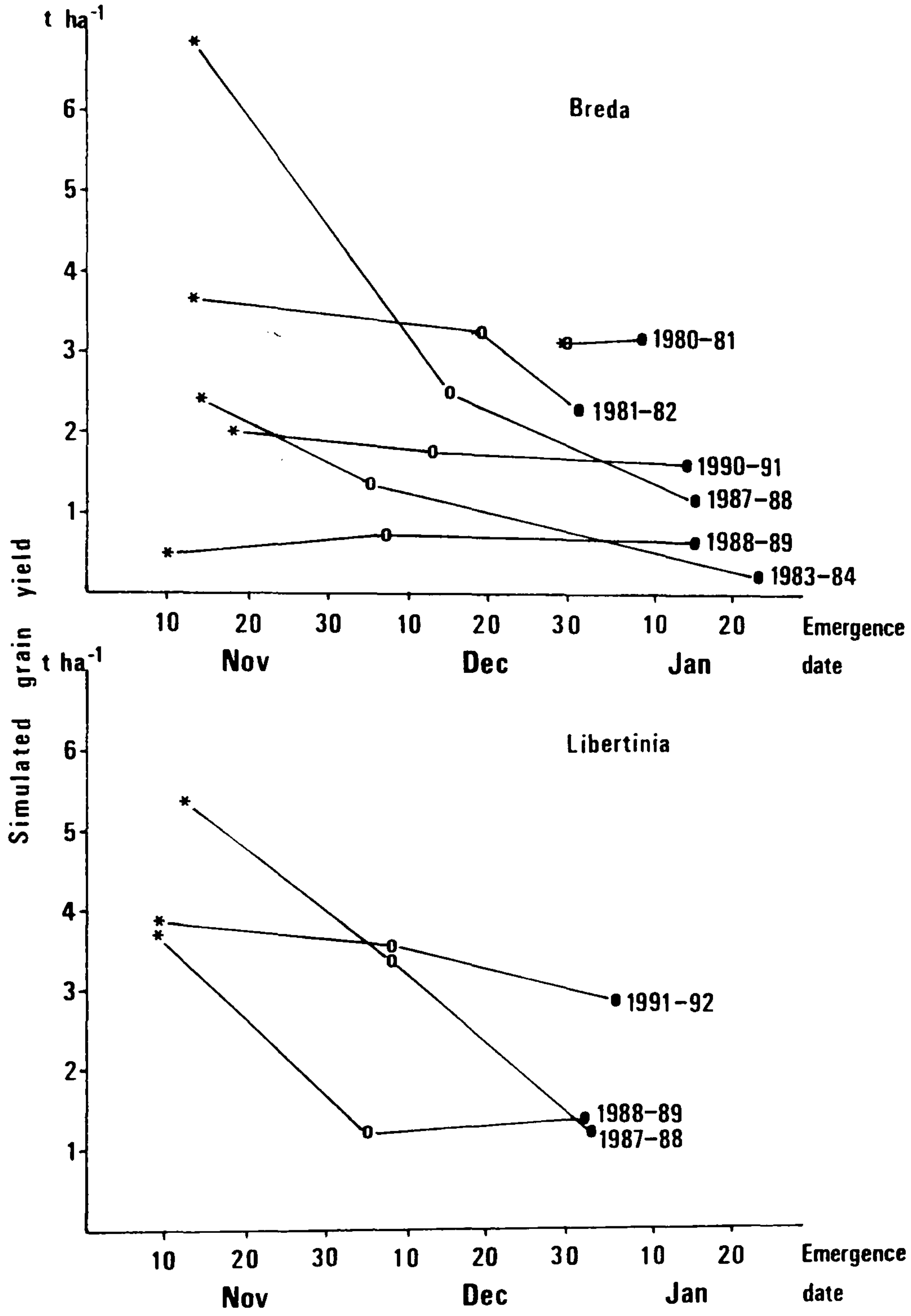

Figure 11. Response to sowing-date for some individual seasons of the cultivar '83022' at Breda, northern Syria, and Libertinia, eastern Sicily. The symbols represent the three sowing dates: * = 1 November, o = 26 November, • = 20 December.

nia, while in some years yields even increased slightly. Stapper and Harris (1989) reported a maximum reduction for individual seasons of 100 kg ha^{-1} day^{-1} delay in germination during November. Examples of the simulated seasonal variation in response to sowing date of '83022' at both locations (the results of '10926' were similar to these) are presented in Figure 11. The sowing-date response is determined by the germination and emergence dates and the total quantity and distribution of rainfall during the season. At Breda, the largest grain-yield reduction with delayed sowing occurred in the wettest season in which rainfall was distributed evenly throughout (1987-88). Another marked reduction of simulated grain yield with delayed sowing occurred in the season 1983-84 in which drought spells during December and February delayed plant development after "normal" and "late" sowings, and a drought spell in May mainly affected the "late" sowing which had its grain filling during that period. In 1980-81 a severe drought in autumn caused the emergence of the "early" sowing to occur at the same time as that of "normal" sowing. December had good rainfall and the rest of the season had no evident stress, which ensured good yields for the three sowing dates. The season 1981-82 had a moderate reduction of grain yield only for the "late" sowing, due to a slightly below-average rainfall in February-March which followed very good precipitation early in the season. Little response to sowing date was observed in 1990-91, which had a poor start but favourable late rains (March through May), and in 1988-89, which was very dry in spite of good early rains.

Most of the patterns of response to seasonal amount and distribution of rainfall mentioned here were similar to those reported by Stapper and Harris (1989) for a comparable environment.

At Libertinia (Figure 11) the largest reduction of simulated yield with delayed sowing occurred in seasons with adequate and even rainfall such as 1987-88 (1990-91 had a similar response: data not shown). The season 1988-89 was characterised by very high rainfall in November and December, followed by low precipitation in the remaining months, which caused the yield of "normal" and "late" sowing dates to be much lower than that of the "early" sowing. The season 1991-92 showed a relatively small yield response to delayed sowing, as severe, intermittent drought occurred in November, February and March probably affecting all three sowing dates in a similar manner.

At Breda, the earlier genotype '10926' had an average yield advantage of about 4% over '83022' across sowing dates, while the reverse occurred at Libertinia where '83022' showed a similar yield advantage. The smallest difference between cultivars at both localities occurred for the "early" sowing (about 3%). The results reinforce the hypothesis that a certain level of earliness may be useful in the long-term, especially in the most marginal environments like Breda. While noting the rather limited difference of yield between '10926' and '83022' at Breda, it should once again be stressed that the latter genotype seems particularly suited for this environment. Nonetheless, with a "normal" sowing the yield advantage of '10926' was present in eight seasons out of 12 at Breda. It was noted that in most cases the superiority in terms of yield was associated with a lower incidence of water stress between the end of ear growth and the beginning of grain filling (growth stage 4). That was confirmed by the correlation between the water stress factor at various stages and grain yield (Table 30), which showed that the stress at stage 4 is the most negatively related to grain yield for all three sowing dates at Breda. This stage, during which flowering takes place, is considered to have a major impact on the number of grains per plant (Ritchie, 1991). Much of the assimilate produced during this stage is stored in the stem and other organs for later retranslocation to the kernels (Ritchie, 1991). The behaviour of the two cultivars was very similar as regards these correlations (data not shown), with a few exceptions. The later maturing genotype ('83022') was more sensitive than '10926' to water stress in the stage 'end of ear growth - beginning of grain filling' (stage 4) with a "late" sowing. Cultivar '10926' was more sensitive to water stress during grain filling, particularly with an "early" or "late" sowing.

At Libertinia, the effect of water stress during grain filling increased with delayed sowing, becoming the only stress factor significantly correlated to grain yield in the case of "late" sowing (Table 30). As at Breda, the genotype '10926' was somewhat more sensitive than '83022' to this final stress when sown on 1 November.

Mean values of the predicted water stress factor at various stages of crop growth and averaged across these stages for the three sowing dates at each location are reported in Table 31. Breda had a consistently higher stress index than Libertinia across the various stages, while at both sites a trend was evident of increasing water stress on delaying the date of sowing. As expected on the basis of its climatic characteristics, Breda is always severely stressed during grain filling, regardless of the sowing date. It appears, therefore, essential to ensure (compatibly with the risk of late frosts) that the beginning of grain filling occurs during a period of less intense stress. It is worth noting that the cultivar with a shorter crop cycle ('10926') had a slightly but consistently lower stress index than '83022' at Breda for each sowing date (data not shown).

Simulated grain yields were correlated with rainfall amounts recorded: i) during the cropping season (October-June), ii) between emergence and maturity of each simulation run, and iii) during the last stages of the crop cycle (end of pre-anthesis ear growth to maturity). The correlation coefficients for each sowing date in the two locations are reported in Table 32. At Breda, there was a decreasing effect of total rainfall and rainfall between emergence and maturity on delaying the sowing, while the opposite trend was shown by the rainfall received during the final stages of growth. At Libertinia, it was the amount of late rain which affected grain yield, especially with a "normal" or "late" sowing. As already mentioned, a great variability exists between years at this location for the amount of precipitation in April and May (see Figure 9).

Table 32. Simple correlation coefficients between simulated grain yield and three rainfall amounts for each season of simulation: i) total seasonal (October-June) rainfall, ii) rainfall between emergence and maturity, and iii) rainfall during the last two stages of growth (stage 4 and 5, see Table 30 for definitions) for three sowing dates at two locations.

Location	Rainfall amount	Sowing date[a]		
		1 November	26 November	20 December
Breda	Total seasonal rainfall	0.87 **	0.75 **	0.55 **
	Rainfall between emergence and maturity	0.77 **	0.69 **	0.61 **
	Rainfall during growth stages 4 and 5	0.50 **	0.72 **	0.88 **
Libertinia	Total seasonal rainfall	0.26 ns	0.09 ns	0.01 ns
	Rainfall between emergence and maturity	0.31 ns	0.26 ns	0.28 ns
	Rainfall during growth stages 4 and 5	0.42 ns	0.90 **	0.89 **

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[a] across cultivars.

ns, ** : not significant and significant at $P \leq 0.01$, respectively.

The effect of anthesis date on grain yield was examined by a partial correlation analysis, the results of which are shown in Table 33. Though the coefficients were not particularly high, it is evident for both cultivars at both sites that the earlier the anthesis (across sowing dates), the higher the simulated yield. Observing the coefficients for the various sowing dates, it appeared that for both genotypes it was very important to have anthesis as early as possible with an "early" sowing, in order to exploit at best the potential of less unfavourable growing conditions, and obtain higher yields. That was particularly true at Breda. However, it must be underlined that in this location the earlier genotype ('10926') when early-sown (1 November) had in five seasons out of 12 an anthesis date before 15 April. This means that phases sensitive to frost, such as late elongation or booting, occurred in a period (end of March-beginning of April) in which late frosts could still be possible (see section 2.1). As already mentioned, even quite mild frosts at these stages may result in severe yield reduction, aggravated by the fact that there is little opportunity for recovery as the crops enter periods of high temperature and water deficit. The rather frequent presence of such risk of frost damage obviously limits the interest in an early variety for early sowing in this cold-prone site, unless the genotype proves rather frost insensitive.

At Libertinia, there also appeared to be a trend towards a favourable effect of earlier anthesis on grain yield for the "normal" sowing date, particularly with the earlier genotype '10926'. There being no realistic risk of frost in this environment, it seems sound that breeding programmes for Sicily should aim to increase the level of earliness in new varieties (Boggini *et al.*, 1990).

Relative to "normal" sowing, the date of anthesis was not advanced by "early" sowing or delayed by "late" sowing as much as the date of sowing was. Moreover, the effect of the different sowing dates on anthesis was different in the two environments, thus providing a clue to a possible interaction between location and sowing date. The results are summarized in Table 34. When sowing occurred

Table 33. Partial correlation coefficients between anthesis date and simulated yield for three sowing dates, two cultivars and each combination of cultivar and sowing date at two locations.

		Location	
		Breda	Libertinia
Cultivar	Sowing date		
	1 November[a]	-0.69 **	-0.48 @
	26 November[a]	-0.24 ns	-0.44 ns
	20 December[a]	-0.18 ns	-0.19 ns
83022	1 November	-0.74 **	-0.65 @
	26 November	-0.14 ns	-0.38 ns
	20 December	-0.26 ns	-0.30 ns
10926	1 November	-0.77 **	-0.51 ns
	26 November	-0.35 ns	-0.59 ns
	20 December	-0.10 ns	-0.13 ns
83022[b]		-0.53 **	-0.63 **
10926[b]		-0.57 **	-0.63 **

---

[a] across cultivars.

[b] across sowing dates.

ns, @, ** : not significant, significant at $P \leq 0.10$ and $P \leq 0.01$, respectively.

Table 34. Mean effect (across seasons) on anthesis date of anticipated ("early") or delayed ("late") sowing relative to a "normal" sowing for two cultivars at two locations.

Location	Cultivar	"Normal" sowing		Difference (days) between "normal" and "early" sowing		Difference (days) between "normal" and "late" sowing	
		Sowing date	Anthesis date	Sowing date	Anthesis date	Sowing date	Anthesis date
Breda	83022	26 Nov	7 May	- 25	- 7	+ 24	+ 4
	10926	26 Nov	2 May	- 25	- 9	+ 24	+ 5
Libertinia	83022	26 Nov	4 May	- 25	- 15	+ 24	+ 7
	10926	26 Nov	1 May	- 25	- 17	+ 24	+ 8

25 days earlier, the date of anthesis at Breda was advanced, on average, by 7 days for '83022' and 9 days for '10926' relative to the average date with "normal" sowing; at Libertinia anthesis with "early" sowing was brought forward, on average, by 15 days for '83022' and 17 days for '10926'. It is evident, particularly for Breda, that the low temperatures in winter slow crop development and growth, thus lengthening the cycle. A further possibility for a longer cycle with "early" sowing could be an early lack of moisture which is sometimes experienced in this environment. As already mentioned, and as reported by Fischer (1984), early sowings do not necessarily germinate upon sowing but must wait until sufficient rains fall. In the present simulation, in one season (1985-86) germination with "early" sowing occurred at Breda 46 days after the date of sowing, and emergence 67 days after sowing. Such constraint did not seem present at Libertinia, where germination was always simulated within one day from sowing.

"Late" sowing caused a delay of anthesis at both localities, but the delay in anthesis date relative to the "normal" sowing was much lower than that of sowing date (which was 24 days). At Breda, the date of anthesis was delayed, on average, by 4 days for '83022' and 5 days for '10926'. At Libertinia, the delay was 7 days for '83022' and 9 days for '10926'. To explain these results it seems sound to postulate that, as expected under Mediterranean conditions, an upper limit to the growth cycle is set by the onset of drought and/or high temperature in late spring (at Libertinia it should mainly be an effect of temperature) which terminate the growing season of winter cereals. At Breda the cycle of both cultivars late-sown (20 December) was shorter than that at Libertinia, confirming the less favourable growing conditions of the former site.

The known differences between the two genotypes in terms of anthesis and maturity were confirmed by the simulation. However, the gap was somewhat reduced at Libertinia relative to Breda (5.3 days for anthesis and 4.3 days for maturity in Syria, on average across seasons and sowing dates; 3.3 days for anthesis and 3 days for maturity, on average, in Sicily). To examine this possible further genotype x location interaction for phenology, the average dates of anthesis across seasons for each combination of location, sowing date and genotype were compared (Table 35). Given the slight difference in latitude between the two sites, the differences in phenology cannot be explained in terms of different photoperiod. They should rather be attributed to the different thermal régime at the two locations. The generally higher temperatures at Libertinia (particularly in winter) hasten anthesis with an "early" and, to a lesser extent, "normal" sowing. In the "late" sowing this hastening of anthesis is probably counterbalanced by a slower fulfilment of the vernalisation requirements of the two genotypes (requirements which are probably more important than one would expect for Mediterranean germplasm (Godwin *et al.*, 1989)), caused by the same higher temperatures of Libertinia. The result is that anthesis date with "late" sowing at Libertinia is equal to, or later than, that at Breda. The response of the two genotypes to the varying environment was different (Table 35). It is interesting to note that the warmer environment hastened the anthesis of the later cultivar ('83022') more than that of the earlier one, in agreement with the findings of Gotoh (1979a, cited in (Boggini *et al.*, 1989)). That caused the already mentioned reduction of the gap between '83022' and '10926' at Libertinia, relative to Breda.

A trend existed for both genotypes at both locations to delay anthesis on increasing the number of days between sowing and emergence of seedlings, i.e., the faster was germination and emergence, the earlier, to some extent, was anthesis. At Breda that was particularly true with the "early" sowing (correlation coefficient between number of days to emergence and anthesis date, $r=0.49$, $P \leq 0.10$, for '83022'; $r=0.53$, $P \leq 0.05$, for '10926'). The reason for this correlation could be the previously-mentioned moisture conditions at sowing at this location. When germination and emergence take place relatively soon after sowing in favourable soil moisture conditions, the crop has good early establishment and

Table 35. Mean anthesis date (across seasons) of two cultivars for three sowing dates at two locations.

	Sowing date					
	1 November		26 November		20 December	
Cultivar	83022	10926	83022	10926	83022	10926
Location						
Breda	30 Apr	23 Apr	7 May	2 May	11 May	7 May
Libertinia	19 Apr	14 Apr	4 May	1 May	11 May	9 May

development leading to faster completion of the cycle. Otherwise, when early drought occurs the whole crop cycle is delayed, as previously described, with a consequent delay in anthesis and maturity. Stapper and Harris (1989) also found a positive correlation between delay in simulated germination and delay in simulated anthesis for northern Syria. "Early" sowing at Breda had the longest period from sowing to germination (11.5 days, average across seasons and genotypes) compared to "normal" sowing (7.6 days) and "late" sowing (4 days).

The comparison between '83022' and the two "dummy" cultivars ('New1' and 'New2') simulated after altering the genetic coefficients of '83022' as described in section 4.2 is summarized in Table 36, the data of which refer to the average across seasons for a "normal" sowing. It can be seen that the reduction of the photoperiod coefficient (P1D), executed to simulate 'New1', resulted at both localities in a marked advance of both anthesis (7 days earlier at Breda, 11 days earlier at Libertinia) and maturity dates (5 days earlier at Breda, 8 days earlier at Libertinia) compared to '83022'. The resulting grain filling period was longer than in '83022', more markedly at Libertinia. 'New1' would substantially simulate the effect of earliness.

On the other hand, an increase of the coefficient for grain filling duration (P5), executed to simulate 'New2', had distinct effects on the phenology of the cultivar in the two environments. At Breda, 'New2' was as early as 'New1' in anthesis, with an intermediate maturity date between '83022' and 'New1'. It could be said that 'New2' simulated the effect of increasing the grain filling period of an early variety ('New1'). At Libertinia, 'New2' had the same maturity date as '83022' and the grain filling period was increased by slightly advancing the date of anthesis. In this case, therefore, 'New2' simulated the effect of lengthening the grain filling period in a non-early cultivar. Such a difference in the behaviour of 'New2' between the two sites is probably due to the restriction of the growing season imposed on a genotype with long grain filling by the severe stress condi-

Table 36. Mean values (across seasons) of cultivar '83022' and two "dummy" cultivars ('New1' and 'New2'), obtained by alteration of some genetic coefficients of the former (see section 4.2 for details), of some predicted characters at two locations simulating a "normal" sowing date (26 November).

	Breda			Libertinia		
Character	83022	New1	New2	83022	New1	New2
Anthesis date	7 May	30 Apr	30 Apr	4 May	23 Apr	30 Apr
Maturity date	30 May	25 May	27 May	30 May	22 May	30 May
Grain filling (dd.)	23.1	24.6	26.8	25.7	28.7	29.7
Rain between emergence and maturity (mm)	181.7	181.3	181.3	258.8	252.2	258.8
Rain during last two growth stages (mm)	21.0	25.4	25.5	51.8	62.3	56.0
Average water stress factor across growth stages (0=min, 100=max)	72.3	61.7	63.9	48.9	39.3	46.7
Grain yield (kg ha^{-1})	1486	1981	2040	3649	4927	4007

tions prevailing at Breda.

The predicted mean values in Table 36 show that at each site each genotype received the same amount of rain between emergence and maturity. 'New1' and 'New2' received more rain than '83022' in the final stages of growth, when rain is particularly important in Mediterranean environments. The advantage of 'New1' over '83022' for this amount of rain was about 20% at both locations, that of 'New2' was about 20% at Breda and 10% at Libertinia. Both "new" cultivars had a lower average water stress index than '83022'. The data for the predicted grain yield show that earliness *per se* had a tremendous effect on productivity in both environments ('New1' outyielded '83022' by about 35%). Increasing the grain filling period of an early variety at Breda had a further small positive effect on grain yield. If the grain filling period is lengthened in a cultivar which is not particularly early, the effect on grain yield is more appreciable: 'New2' had a 10% higher grain yield than '83022' at Libertinia.

Despite the previously discussed limitations that the simulation technique of altering phenology may have, the relevance of the present results is such that the importance of earliness and a long grain filling period cannot be underestimated. Stress escape is confirmed once again (see section 2.4) to be an essential trait under dryland Mediterranean conditions. In practice, the possibility and the consequences of introducing a certain level of earliness into a genetic background which already possesses a possible stress "tolerance", whatever the mechanism(s) might be, deserve further attention. The already mentioned breeding programme active in Sicily (Boggini *et al.*, 1990) is trying to incorporate the earliness and dwarfness (which are related) of modern cultivars into native landraces which possess good levels of stress tolerance.

The effect of a greater soil water content at sowing (ISW) was evident only at Breda (Table 37). At this site, with a "normal" sowing, '83022' had an average yield increase of about 12% when the soil content at sowing was higher. Similar-

Table 37. Average across seasons of the simulated grain yield of two genotypes at two locations (sowing date: 26 November) simulating two different initial soil water (ISW) indexes.

		Simulated grain yield (kg ha^{-1})	
Location	Genotype	ISW index 0.5	ISW index 0.7
Breda	83022	1485	1659
	10926	1560	1781
Libertinia	83022	3649	3619
	10926	3466	3487

ly, '10926' had an average increase of 14% (Table 37). Such positive effect was not present at Libertinia, where the two genotypes had practically the same average simulated yield at the two initial soil water contents.

Considering the simulated data from Breda, the average yield advantage of '10926' over '83022' was greater at higher than at lower ISW (+7% versus +5%).

The different response of the two locations to an increased soil water content at sowing could be attributed to the different effect that such higher ISW has had on the plant available soil water (PAW) through the season in the two environments. At Libertinia, a higher soil water content at sowing conferred an advantage over the lower ISW in terms of plant available soil water only until emergence at most. Later on, the two treatments did not differ for plant available water, and this happened in all the seasons considered. At Breda, in most seasons a higher ISW resulted in a greater plant available soil water content until, at least, the stage corresponding to terminal spikelet initiation (beginning of elongation). In the seasons with drought spells during autumn or winter (e.g., 1980-81, 1982-83, 1985-86) the higher PAW due to higher soil water content at sowing persisted until the end of pre-anthesis ear growth, or to the beginning of grain filling. Only in the seasons with higher total rainfall or with good early rains (e.g., 1981-82, 1987-88, 1988-89) was the advantage in terms of PAW present until emergence at most, as at Libertinia. In the former two seasons of these the simulated yield did not differ between the treatments with higher and lower ISW. It is evident that under the usually very stressful conditions of Breda even a small early increase of soil water content (about 9% in the simulated case: see section 4.2) will improve the yield response later on. For this, and for the reasons previously discussed about the effect of a delayed germination, whenever possible sowing in very dry soil should be avoided in marginal environments like Breda.

In conclusion, it seems that the CERES-Wheat crop model is applicable with a sufficient reliability also under Mediterranean conditions, providing a realistic approach to the genotype x environment interaction within and across growing seasons. It appeared, however, that this model, developed for more favourable conditions, should be modified or better calibrated for the considered area as regards the estimation of extreme conditions, both favourable and unfavourable. It would be advisable to include an estimation of frost damage, particularly of late events, and, as regards durum wheat, of lodging damage when heavy late rain occur.

Such a model could have a major relevance on the definition of the "ideotype(s)" for the target environment, thus assisting the breeders in the selection of parental materials. For this purpose, however, a user- driven definition of important characters should be added to the programme. In its present version, it is possible to modify, as also seen in this study, the phenology of a given genotype, thereby showing for instance, the importance of earliness or of a long grain filling period in that environment. It would be very useful if other adaptive traits were also included, giving priority to those possibly having a relation with the crop's response under moisture-limiting conditions (e.g., peduncle length, awn size, flag leaf size).

5 *Osmotic adjustment*

An experiment was conducted to assess possible differences in osmotic adjustment among durum wheat genotypes. The method described by Morgan (1988) was adopted. This measures the plant responses to water stress during the first week of ontogeny. As underlined by Morgan (1988) determination of any association between variation in growth and the variation in osmotic adjustment of expanding organs was based on the assumption that cell expansion must involve an increase in solutes to maintain turgor as cell volume increases (Cosgrove, 1986). High turgor pressure has been suggested as an indicator of stress resistance (Johnson and Brown, 1977), but it may also be a consequence of changes in growth rate caused by other factors.

Four landraces were chosen for the present experiment. These had shown different behaviour under field drought stress, viz., '83089' from Jordan, '7419' of unknown origin, '5694' and '17870' both from Tunisia. Entry '83089' was taken for its good performance in both seasons of evaluation at Breda (see Table 6) not directly attributable to any stress escape (see Table 14). Conversely, the relatively high yield of '7419' in 1989-90 should be mainly due to its distinct earliness (see Table 14). It would have been interesting to test entry '10926' which was characterised by good performance and significant earliness in both seasons at Breda (see Table 6 and 14) but the poor germination of the available sample did not permit using it. Entry '5694' presented a low yield in both seasons (Table 6), possibly suggesting a poor adaptation to the environment. The fourth landrace ('17870') was not one of the 75 which were included in the previously described field study, but was included in this experiment because of its interesting features revealed in different field trials under the same environmental conditions (Annicchiarico and Pecetti, 1993; Pecetti and Annicchiarico, 1993). This landrace showed a good and stable yield and possessed attributes under stress such as relative lateness, tall stature and outstanding kernel weight which suggested a possible tolerance to the stress.

Sixty seeds of each line were soaked for 15 minutes in 5% (w/w) solution of sodium hypochlorite to eliminate possible fungi and then rinsed in flowing tap water for 30 minutes. The 60 seeds were split into two groups of 30, each sown in a 'Magenta' type dish on a 6 x 6 cm capillary matting pad moistened with 10 ml of distilled water. The eight dishes were placed at random in a Fison 600 THTL growth cabinet maintained at 22° C with 16 hrs. photoperiod. On the morning of the fourth day after sowing shoot and longest root length were measured on four seedlings from each dish, taken at random and marked after the measurement. Subsequently, half of the dishes (one for each genotype) were assigned at random to the control treatment and were watered with a further 10 ml H_2O each. The remainder were assigned to the stress treatment and received 10 ml each of 20% (w/w) polyethylene glycol (PEG) 8000 solution. After 48 hrs., shoot and longest root length were again measured on the same four seedlings per dish, and water potential (Ψ) was determined by the dye (or Chardakov's) method (Salisbury and Ross, 1992). This is a simple and easily learned method, which requires no elaborate or expensive equipment and can be used in both the laboratory and the field. The dye method seems suitable to measure relative values and to indicate differences in leaf water potential (Knipling and Kramer, 1967). The method depends on changes in densities of known solutions as tissues immersed in these solutions absorb or lose water by osmosis. If the density of a given solution does not change (no water exchange occurs), this solution has the same water potential as the tissues in it. It is assumed that solute movement between tissue and surrounding solution is negligible. In the present experiment, after a preliminary assessment of the possible ranges of water potential under both the control and the stress treatment, two series of 6 test tubes containing sucrose solutions at 20° C of known concentration were prepared for each line: one series for the control and one for the stress treatment. Each solution was then split into two parts, one of which was coloured by adding a few crystals of methylene blue. Some shoots were excised at random from each dish, cut into small pieces, mixed together and subdivided into the test tubes with different coloured solutions. After a period of 15-20 minutes, sufficient to allow an exchange of water (Salisbury and Ross, 1992), a drop of each coloured solution in which the tissue samples were immersed was added to the corresponding non-coloured solution. The solution in which the coloured drop neither sank nor rose, indicating that no water exchange occurred between the coloured solution and the tissue sample, was observed or estimated. From the known concentration of such solutions, the water potential of the immersed leaf samples was determined from tabulated values (Ross, 1974). The same operation was conducted on the roots of the same seedlings. At the end of the sequence, therefore, shoot and root water potential of both control and stress treatments were determined for the four genotypes. All the other seedlings not used in each dish (usually 10 to 15) were split into shoots and roots, the bulks of which were placed in Eppendorf tubes and rapidly frozen. After thawing the tissue and expressing the sap, the sap and tissue were separated by centrifugation. Ten μl of the supernatant were used for osmometry. The osmotic potential (π) of cell sap was determined by a Wescor 5100B vapour pressure osmometer.

Given the time-consuming procedure for the determination of Ψ, it was not possible to make within a reasonably brief span of time more than one measurement for any genotype x treatment x part of the seedling combination. Therefore, it was decided to repeat the measurements at different times, thus creating replicates in the time instead of in space. The whole sequence of the above-mentioned operations from the washing of the seeds to the measurements was integrally repeated during three consecutive weeks, keeping constant from week to week any single factor involved. The three periods constituted statistically as many blocks of the experiment which could therefore be analysed as a randomised complete block design. The shoot and root lengths measured on four seedlings per dish in each week were averaged over each dish so that one value of length was associated to one value of Ψ and one of π in each combination: genotype x treatment x part of the seedling x replication. The frozen samples from the first and second week for the π measurement were kept as such until the samples from the third week were also frozen. Then the three replications of the samples were thawed all together, crushed, centrifuged and measured by the osmometer. The instrument was re-calibrated every ten samples by a standard solution of known osmolality. The osmotic potential was determined twice in each sample, the first time following a random serial order of the samples and the second time inverting such order. Later it was observed that the correlation between the values observed in the two series of readings was very high ($r=0.99$, $P<0.001$) and, therefore, these values were averaged for each sample. Turgor pressure (P) was finally calculated as:

$$P = \Psi - \pi \text{ (Morgan, 1988).}$$

All lengths were expressed in mm and all water relations parameters in MPa. Beside the shoot and longest root length measured at 48 hrs., the difference of length between the second and the first measurement was also considered, indicating the growth ability during the stress imposition (Morgan, 1988). However, differences in growth under stress among lines could not only be attributed to different responses to the stress but also to intrinsic genetic differences in growth rate among genotypes. To minimise this risk of bias, an adjusted growth was calculated as:

$$(\text{growth under stress/growth in the control}) \times 100 \ .$$

All variables were subject to ANOVA and line mean values compared by Duncan's multiple range test. Simple correlation coefficients among traits were also computed.

No significant differences among lines were detected in the control treatment concerning any variable, both in the shoots and in the roots. For instance, the extreme values recorded in the shoots were -0.73 and -0.76 MPa for Ψ, -0.97 and -1.05 MPa for π, 0.22 and 0.38 MPa for P, 28.3 and 38.9 mm for the growth. Conversely, differences existed among genotypes in the stress treatment for osmotic potential and turgor mainly at the shoot level (Table 38). Shoot water potentials of the landraces ranged between -1.35 and -1.48 MPa but did not differ significantly. According to Blum (1989) this is an important requisite for evaluating genetic variation in osmotic adjustment, as the rate of adjustment may vary according to leaf water potential. It must be noted that a positive association, although not significant at the 5% threshold, existed between water potential and osmotic potential.

Entry '83089' possibly possessed the ability to osmotically adjust in the presence of the stress. Indeed, while its shoot water potential under stress was comparable (though being the lowest) to that of the other lines, its osmotic potential was significantly the lowest and, therefore, its turgor pressure was significantly the highest. Turner and Jones (1980) suggested that the degree of osmotic adjustment can be measured as the change in osmotic potential at a given water potential. Thus, '83089' maintained the shoot turgor pressure at reduced water potential: while Ψ decreased from -0.75 to -1.48 MPa because of the stress, P was 0.22 MPa and 0.37 MPa in the control and under stress, respectively. However, the line which maintained the most turgor had also the least growth (both absolute and adjusted growth) (Table 38). This result is in disagreement with Morgan (1988) and with Blum (1989). The former author found differences in osmotic adjustment between genotypes of bread wheat (*Triticum aestivum*) which were consistent with differences in coleoptile growth under water stress and with previously assessed differences in osmotic adjustment at an adult stage under field

Table 38. Mean lengths of roots and shoots in four durum wheat genotypes subject to water stress, and relative water relations. Lengths are expressed in mm, water relations in MPa.

Entry	Water Potential	Osmotic Potential	Turgor Pressure	Length 1[a]	Length 2[b]	Growth[c]	Adjusted[d] Growth
Roots							
F-test[e]	ns	@	@	@	ns	ns	ns
17870	-1.45 a	-1.14 a	-0.31 b	41.3 ab	53.0 a	11.7 a	88.0 a
83089	-1.63 a	-1.82 b	0.19 a	35.0 b	55.0 a	20.0 a	90.3 a
7419	-1.56 a	-1.35 ab	-0.21 b	42.1 ab	63.5 a	21.4 a	87.3 a
5694	-1.48 a	-1.51 ab	0.02 ab	43.7 a	58.7 a	15.0 a	81.0 a
Shoots							
F-test[e]	ns	*	*	*	**	*	*
17870	-1.35 a	-1.18 a	-0.17 b	32.8 a	53.1 a	20.3 a	76.3 a
83089	-1.48 a	-1.85 b	0.37 a	13.8 c	22.3 c	8.5 c	21.3 c
7419	-1.40 a	-1.38 a	-0.02 b	22.4 bc	38.6 b	16.2 ab	48.3 b
5694	-1.47 a	-1.47 a	0.01 b	24.6 ab	36.1 b	11.4 bc	35.0 bc

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[a] before stress imposition.
[b] 48 hrs. after stress imposition.
[c] length 2 - length 1.
[d] (growth under stress/growth in the control) x 100.
[e] among entries; ns, @, *, ** : entry means not different, different at $P \leq 0.10$, ≤ 0.05 and ≤ 0.01, respectively.

Entry means followed by the same letter within each variable and each part of plant are not different at $P \leq 0.05$ according to Duncan's test.

conditions. Blum (1989) observed a negative association across barley (*Hordeum vulgare* L.) genotypes between osmotic adjustment and growth reduction by PEG-induced drought stress. Conversely, Quisenberry *et al.* (1984) reported a highly significant negative relationship between turgor maintenance and shoot growth in cotton (*Gossypium hirsutum* L.) under field drought stress. They proposed three explanations to interpret their results: i) growth inhibition and turgor maintenance are both manifestations of water stress, i.e., parallel but not related responses; ii) the accumulation of osmotically active solutes is at the expense of some growth processes; iii) the materials with low shoot growth may have put proportionally more dry weight into roots. It is interesting to remark that in the present experiment '83089' had one of the longest root growths (the longest, considering the adjusted growth) (Table 38), and this seems to agree with the mentioned third argument of Quisenberry *et al.* (1984). In other cases growth could not be correlated with turgor (Pritchard and Wyn Jones, 1986; Termaat *et al.*, 1985), or turgor remained constant during exposure to water potentials that were low enough to inhibit growth (Meyer and Boyer, 1981; Michelena and Boyer, 1982). Grumet *et al.* (1987) also observed that lower solute potential was associated with reduced growth in barley isopopulations. Besides proposing as possible explanations of their finding a metabolic cost to obtain a lower osmotic potential, or an impairment between the total metabolic function and the cell growth at low osmotic potential, these authors suggested the action of highly pleiotropic genes which simultaneously may influence growth and solute potential. Grumet *et al.* (1987) highlighted the different genetic nature of the osmoregulatory trait between their materials (which had a constitutively low osmotic potential) and the genotypes used by Morgan (1988) (in which the osmotic adjustment was induced by the stress conditions), and attributed a certain role to such difference in accounting for the contradiction between their results and those obtained by Morgan (1988). Blum (1989) stressed the fact that induced osmotic adjustment may be an important attribute of drought resistance while the worth of the constitutive adjustment should be re-assessed. In the case of the present investigation, '83089' did seem to possess an induced adjustment, as its root and shoot osmotic potential, not different from that of the other lines in non-stress conditions, became indeed the lowest under water stress (Table 38).

The behaviour of '83089' and the opposite one of '17870' certainly accounted for the positive relationship between osmotic potential and shoot growth under stress ($r=0.94$, $P=0.06$, with growth; $r=0.93$, $P=0.07$, with the adjusted growth), i.e., the higher (= less negative) π, the larger the growth. In fact, '17870' showed the highest osmotic potential under stress (-1.18 MPa) and the highest adjusted shoot growth (76%). Keim and Kronstad (1981) found significant positive association of osmotic potential with grain yield in bread wheat. It is remarkable that the high π value of '17870' resulted from the lack of substantial osmotic adjustment. The difference between the shoot osmotic potential under stress and that in the control was 0.88 MPa for '83089', 0.46 MPa for '5694', 0.33 MPa for '7419' and only 0.18 MPa for '17870'. However, assuming the values of π are accurate (as mentioned, the osmometer was frequently checked against known solutions during the measurement process), a dilution of protoplasm by cell wall water during the sap extraction of '17870' should not be neglected. As water diffuses across the membrane in a real system, it not only causes an increase in pressure but also dilutes the solution. This increases the osmotic potential in the solution (makes it less negative), so the pressure required to reach equilibrium is less than it would have been predicted from the original osmotic potential (Salisbury and Ross, 1992).

The correlation analysis revealed a noticeable positive correlation between water potential and growth ($r=0.99$, $P=0.01$ with growth; $r=0.98$, $P=0.02$ with the adjusted growth). That is, the higher (=less negative) the water potential maintained under stress, the better the growth. It was essentially the entry

'17870' that coupled the best growth under stress with the least reduction of Ψ relative to the watered control. This result might be a clue for a possible drought "avoidance" by this landrace in the sense suggested by Levitt (1972) of ability to endure periods of drought whilst maintaining a high plant water status. Seropian and Planchon (1984) observed this kind of behaviour in two durum wheat lines derived from landraces originating from the middle east ('Haurani') and Tunisia ('Bidi'). It is worth remarking that the entry '17870' is one accession from the Tunisian landrace 'Mahmoudi'. As previously mentioned, Turner (1979) refers to such "avoidance" as "drought tolerance with high tissue water potentials" which is accounted for by either reduction of water loss (e.g. *via* increase in stomatal resistance or reduction of radiation absorbed) or maintenance of water uptake (e.g. *via* increased root density and depth).

In conclusion, the two entries which were included in the experiment because of their promising field performance under drought stress showed substantially contrasting physiological mechanisms. No information, however, was available on their water status under actual field conditions to which the results of the present study could be related. It would seem that their good adaptation to drought is due to either of the physiological mechanisms possessed at the seedling stage (tolerance for '83089', avoidance for '17870'). That implies, of course, that the osmotic adjustment shown at this stage by '83089' is somewhat positively related to its behaviour at the adult stage, in spite of its negative relationship with the growth at the seedling stage. Otherwise, its possible superiority would rely on other mechanisms than stress tolerance through osmotic adjustment.

The present investigation indicates that the assessment of the osmotic adjustment ability under stress in the early stages of ontogeny does not seem unequivocally acceptable as a selection criterion to discriminate the best durum wheat genotypes under field moisture-limiting conditions.

6 *Salinity experiments at ICARDA*

6.1 *Field assessment of salinity resistance: Hegla 1985-86*

A set of 3950 durum wheat accessions from the ICARDA collection was evaluated during 1985-86 in northern Syria for several morpho-agronomic traits, including salinity resistance under natural conditions (Damania *et al.*, 1987; Annicchiarico and Pecetti, 1988). This latter screening was carried out at a salt-affected field nursery site at Hegla (55 km SE of Aleppo) near the shoreline of the Jabboul salt lake. The soil is calcareous and highly saline, the salt consisting mainly of sodium and chloride ions (A. Matar, pers. comm.). The salt concentration increases greatly with soil depth and rooting depth is, therefore, shallow. The long-term mean annual rainfall is about 200 mm, and the amount of precipitation in 1985-86 was 188 mm. The site is obviously drought-affected as well as saline. Soil salinity levels in the experimental field had been reported as highly variable (Jana *et al.*, 1983).

The magnitude of the experiments and the availability of only a low amount of seed precluded the use of more than one replicate when large numbers of entries were involved in our evaluation trials. A partial solution to these problems was achieved by using the modified augmented design proposed by Lin and Poushinsky (1983) or the augmented design (Federer, 1956). Both designs permitted the non-replicated recorded values to be adjusted, and differences among evaluated accessions to be tested, on the basis of the performance of check entries replicated several times in different "blocks" throughout the experiment (Pecetti *et al.*, 1992b).

The reason for that choice was the need to realise a compromise between experimental accuracy on the one hand and experiment manageability and cost limitations on the other hand. The modified augmented design was also adopted at Hegla (Annicchiarico and Pecetti, 1988). However, being conscious of the difficulty of coping with the soil heterogeneity of this site, the whole experiment was sown twice in order to obtain for the adjusted data of each entry, two replications, if not statistically at least practically. The locally adapted landrace 'Haurani' was used as the check cultivar replicated several times in the trial. This landrace had already been used as the check variety in the same environment (Jana *et al.*, 1983, Weltzien and Winslow, 1984) and, although not being rated for its response to salinity, it was not much worse performing than a supposedly tolerant check (Weltzien and Winslow, 1984). Unfortunately, the field conditions did not allow the best exploitation of the adopted design. Indeed, there were bare salt encrusted spots where materials died including 'Haurani', thus making impossible a proper data adjustment throughout the trial. Observations were recorded on early growth vigour at the 5-6 leaf stage and on the general plant appearance before maturity. The latter criterion was rated on the basis of a 9-level agronomic score derived from the one adopted for drought tolerance screening (Annicchiarico and Pecetti, 1990) and modified to give greater relevance to the ability by the plants to normally head and set grains. It was observed that the salinity caused irreversible damage to the plants at two distinct stages besides the seed germination, i.e., just before stem elongation and during the heading. In the same environment, spike fertility reductions of about 80% were observed even on previously selected materials (Weltzien and Winslow, 1984). The visual assessment of performance under stress, represented by the agronomic score, was further complemented by the measurement of the total above-ground biomass (TAB). Given the characteristic arrangement of the plots in the modified augmented design, which ensures that each entry is sown close to at least one check cultivar, and the above-mentioned impossibility of making an overall adjustment on the basis of the design, the performance of each accession was judged relatively to that of the nearest check. In particular, the accessions presenting in both 'replications' a higher agronomic score than the check coupled with a TAB superior to that of the check entry by 10% or more were noted as possibly salt tolerant. Altogether 332 accessions were identified as such from the collection. However, the patchy aspect of the field made me feel this number would be an overestimate. It could have logically been argued that a greater number of replications would have improved the selection efficiency. Jana *et al.* (1983) used three replications when they tested durum wheat entries in the same locality, but when the entries they had tentatively classified as salt-tolerant were again assessed by Weltzien and Winslow (1984), adopting eight replications, significant differences of response to the stress were evidenced. Yet, I felt it was not only a matter of number of replications which made the selection questionable in such an environment, and that feeling had come out since the development of the experiment. For this reason, at plant maturity, several spots were identified in the field (measuring approx. 75 m x 40 m) with varying crop appearance from no evident salt damage to bare land with salt incrustation on soil surface. Within these spots, a plot of the check cultivar 'Haurani' was empirically identified, the general conditions of which did not differ too much from the average of the other entries in the same spot. A soil sample to a depth of 30 cm was taken immediately adjacent to each remarked plot of 'Haurani' and its electrical conductivity of the saturation extract (EC_e) was later measured at the ICARDA's soil laboratory. Fourteen soil samples were collected from within the field (Figure 12). The 14 plots of 'Haurani' next to the sampling points represented as many replications of an hypothetical variety to be tested. The EC_e values of the samples are indicated in Figure 12: they varied between 1.3 and 52.9 dS m^{-1}, which is a range not uncommon in salt-affected fields (Richards, 1983b). As already noted by Richards (1983b), wide differences may occur over a

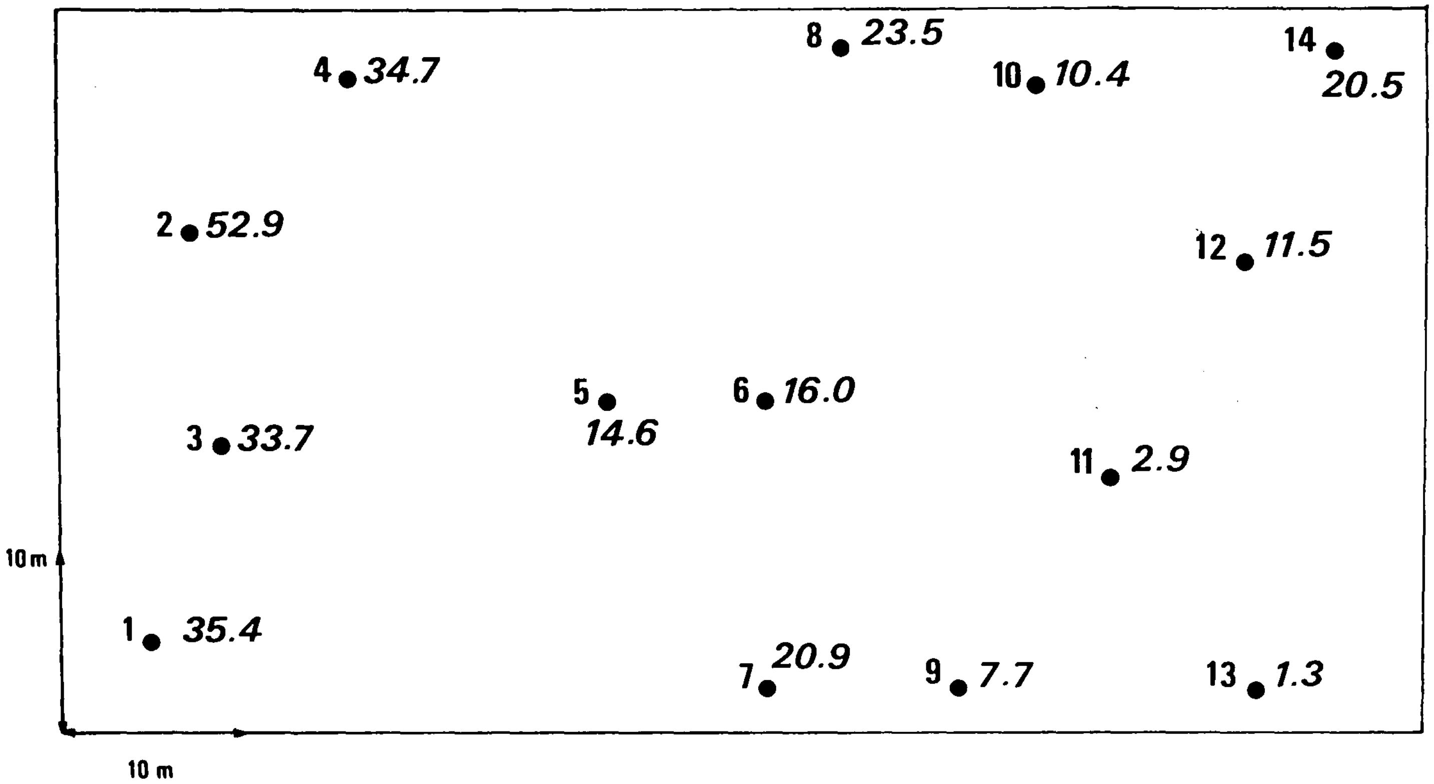

Figure 12. Scheme of the field used at Hegla, northern Syria, to screen durum wheat germplasm against naturally occurring salinity. The dots represent the position of 14 soil samples collected next to as many plots of the control cultivar 'Haurani'. In roman type is the sample number; in italic type is the measured electrical conductivity (dS m^{-1}) for each sample.

distance of only a few meters horizontally. For instance, there were about 11 m between sample 7, whose EC_e was beyond the limit of 20 dS m^{-1} at which growth in wheat is considered to cease, and sample 9 which had an EC_e of 7.7 dS m^{-1} thought to cause about 10% yield decrement in wheat (A. Matar, pers. comm.). Approximately nine m separated samples 8 and 10, where the former had more than double the EC_e of the latter. Comparing my personal experience of the field with the site descriptions made by Richards (1983b), Hegla likely coincided with the situation referred to as 'extreme' by this author. In this kind of field, Richards (1983b) observed 27% of land completely bare and 23% which had normal production; 82% of the total yield was expected to come from only 49% of the land.

The plot of 'Haurani' next to sample 2 had died soon after emergence. For the remaining 13 check plots correlation coefficients were computed between EC_e, early growth vigour score, agronomic score and total above-ground biomass. There was a strong negative relationship between the three agronomic traits and soil salinity (Table 39). It is evident that since the early stages of development the stress markedly affected the crop growth. The fact that the agronomic score had a stronger correlation with EC_e than the total biomass is not surprising, as the latter character measured whatever the biomass was, even only leaves and stems, while the former, as previously mentioned, was carefully attributed on the basis of spike formation and seed setting which are very sensitive phases to salinity. The present results are in agreement with those of Richards (1983b) who found an average $r^2 \approx 0.75$ between grain yield and EC_e in winter cereals.

Such variation of the plant response is troublesome for breeding, as it inflates the environmental component of variation relative to genetic variation, making evaluation and selection very difficult. Even a high number of replications in such fields does not allow the selection of the most tolerant entries but only, at most, of those with the highest yield potential in the least saline areas. Richards (1983b)

Table 39. Correlation coefficients (r) between early growth vigour at 5-6 leaf stage, agronomic score before maturity and total above-ground biomass recorded on 13 plots of the control cultivar 'Haurani', and electrical conductivity of the saturation extract (EC_e) of as many soil samples collected adjacent to each cultivar plot. Hegla 1985-86.

	r between EC_e and
Early growth vigour	-0.77 **
Agronomic score	-0.82 **
Total above-ground biomass	-0.70 **

**: $P \leq 0.01$

concluded that the best breeding strategy to improve the overall yield of crops growing on patchy soils is to select for high yield on non-saline soils. To reinforce this strategy there is evidence that the highest yielding cultivars at low salt levels may be the same as those that yield best in non-saline soils in the same region, presumably because of the overriding influence of yield potential (Richards *et al.*, 1984, cited in (Richards, 1983b)). This concept was formalised by Rawson *et al.* (1988) who enuntiated a two-fold origin of tolerance: 1) a physiological tolerance, defined as a small relative reduction in growth due to salinity; and 2) an absolute tolerance, shown as an intrinsic high growth rate of the genotype, both in and out of salinity. These authors proposed that more emphasis should be placed on the latter tolerance while selecting.

In conclusion it is likely that the accessions tentatively classified as tolerant at Hegla in 1958-86 would have simply owed their superiority to the fact that they were growing on less saline spots. On the basis of the afore-mentioned conclusions of Richards (1983b) and Rawson *et al.* (1988) it could be wondered whether they had a superior performance to the other entries under more favourable conditions, which could account also for a higher yield under more saline conditions. Unfortunately, there are no data available on the yield potential of all entries in non-saline soil in the same environment. On the other hand, in an experiment carried out later under controlled conditions (the results of which will follow in section 6.2.1.2) a sample of the entries tentatively classified as 'tolerant' and a sample of those classified as 'susceptible', grown in the same saline medium, did not differ for any of the recorded agronomic characters. This result made me think once more that the selection carried out at Hegla was little, if at all, effective.

Salinity poses practical problems for researchers in ensuring a known and uniform stress for all the plants being screened. In this context the field is the least satisfactory experimental location because of the large temporal and spatial variations in salt concentrations and because of the interaction of salinity with other environmental factors such as water availability. Field evaluations have demonstrated large standard errors of mean performance in saline conditions, which reduce the power of statistical tests and hinder discrimination on the basis of such tests. Selection for grain yield is inefficient because of its low heritability under stress in field conditions (Fischer and Maurer, 1978; Blum, 1982). Screening large numbers of genotypes on naturally saline soils does not seem, therefore, feasible. Uniformly salinized soils may be unobtainable unless synthesized, which then may cause the problem of cost for large scale evaluations. Francois *et al.* (1986) were able to evaluate two wheat cultivars under six salinity treatments by irrigating field plots with salinized water. Aragüés *et al.* (1992) obtained controlled field salinity conditions by using a triple-line-source sprinkler system to establish a linear salinity gradient of time-weighted irrigation water electrical conductivity from 2.4 to 14.2 dS m^{-1}, in which four entries were evaluated.

To avoid the variability encountered in field screening programmes and to control the salt levels, plants are often grown in nutrient solution to which NaCl is added. In most of these experiments it is survival and/or short-to-medium-term growth rather than grain yield which is adopted as an indicator of stress resistance (e.g., McGuire and Dvorák, 1981; Sayed, 1985; Kingsbury and Epstein, 1986, 1988; Muhammed *et al.*, 1987; Bizid *et al.*, 1988; Rawson *et al.*, 1988; and several of the above-mentioned studies by Dr. J. Gorham and colleagues in Bangor, UK).

Because a plant's salt injury depends on its ontogenetic stage as well as on the nature and severity of previous stresses (the role of "ontogenetic drift" in plant response to salt stress has been emphasized by Shannon (1984)), it is sometimes desirable to measure responses to salt stress at different growth stages.

The preceding methodology has been adopted in the following experiments.

6.2 *Greenhouse assessment of salinity resistance with sand-culture technique: Tel Hadya 1989-91*

Three greenhouse experiments were carried out at ICARDA's headquarters (Tel Hadya, Syria) between 1989 and 1991 with the purpose of evaluating for salt resistance under controlled conditions genetic resources of durum wheat from the available collections.

6.2.1 *Experiment Tel Hadya 1989*

6.2.1.1 *Materials and methods*

Three galvanized steel tanks, each 1 m x 2 m x 0.8 m deep, were constructed at ICARDA and used for screening of durum wheat accessions in the greenhouse. The tanks were lined with polythene film. A non-calcareous gravel layer of about 5 cm was placed at the bottom and the rest was filled with pure quartz sand. A solution was circulated containing the desired salt level and the nutrient solution prepared with 0.5 g l^{-1} of 'Phostrogen' (Phostrogen Ltd., Corwen, Clwyd, UK) (containing 0.52 g l^{-1} NO_3^-, 0.16 g l^{-1} PO_4^{3-}, 0.27 g l^{-1} K^+, 0.03 g l^{-1} Ca^{2+}, 0.02 g l^{-1} Mg^{2+} and 0.007 g l^{-1} Na^+), plus NaFeEDTA (0.02 g l^{-1}) and 0.6 ml l^{-1} of a stock micronutrient solution (containing 2.86 g l^{-1} H_3BO_3, 1.81 g l^{-1} $MnCl_2.4H_2O$, 0.22 g l^{-1} $ZnSO_4.7H_2O$, 0.08 g l^{-1} $CuSO_4.5H_2O$ and 0.02 g l^{-1} $H_2MoO_4.H_2O$). This solution was circulated in each tank twice a day by a centrifugal pump. Two hundred litres of solution were applied to each tank during each turn of irrigation through a series of dripping lines (one every 20 cm). The solution drained by gravity into plastic barrels partly buried below each tank, from where it was pumped up again (see Figures 13 and 14 for a general view and a detail of the apparatus). The solution was monitored weekly for electrical conductivity (EC) and afterwards replaced by a fresh one. Three salt treatments were used in this experiment, one in each tank: 1) a control with no salt, 2) 100 mol m^{-3} NaCl, and 3) 200 mol m^{-3} NaCl. Salt was added to the nutrient solution starting on the 14th day after germination, when the seedlings were well established, and increasing 25 mol m^{-3} day^{-1} until the required salinity had been reached. $CaCl_2$ was added in the second and third salt treatment to maintain a nominal Na:Ca ratio of 20:1 (ignoring the small amount of Ca and Na present in the nutrient solution), in order to avoid the confounding effects of concurrent increase in Na/Ca ratio and in NaCl (Greenway and Munns, 1980).

A set of durum wheat accessions was chosen to represent a diversified geographic origin as well as a variable agronomic response to naturally occurring abiotic stresses such as drought and frost. Six entries provisionally classified as salt tolerant and six as salt susceptible on the basis of the field experiment carried out at Hegla (section 6.1) were also included. In total, 34 entries originating from 10 countries and including also the old variety 'S. Cappelli' and the modern variety 'Sham 1' were evaluated. A completely randomised design was adopted with five replicates per treatment. Each entry was represented in each replication by two plants, one of which was harvested at an early stage for the determination of shoot weight and leaf area, and one grown to completion of the cycle to record other morpho-physiological traits. The initial planting distance was 5 cm apart; the final distance, after the early harvest, was 10 cm apart. Seeds of all 34 entries were vernalised for two weeks in September 1989 at a temperature of 2° C. At the beginning of October they were sown in the three tanks placed in a greenhouse. Six weeks after germination and at least four weeks after full salinity had been

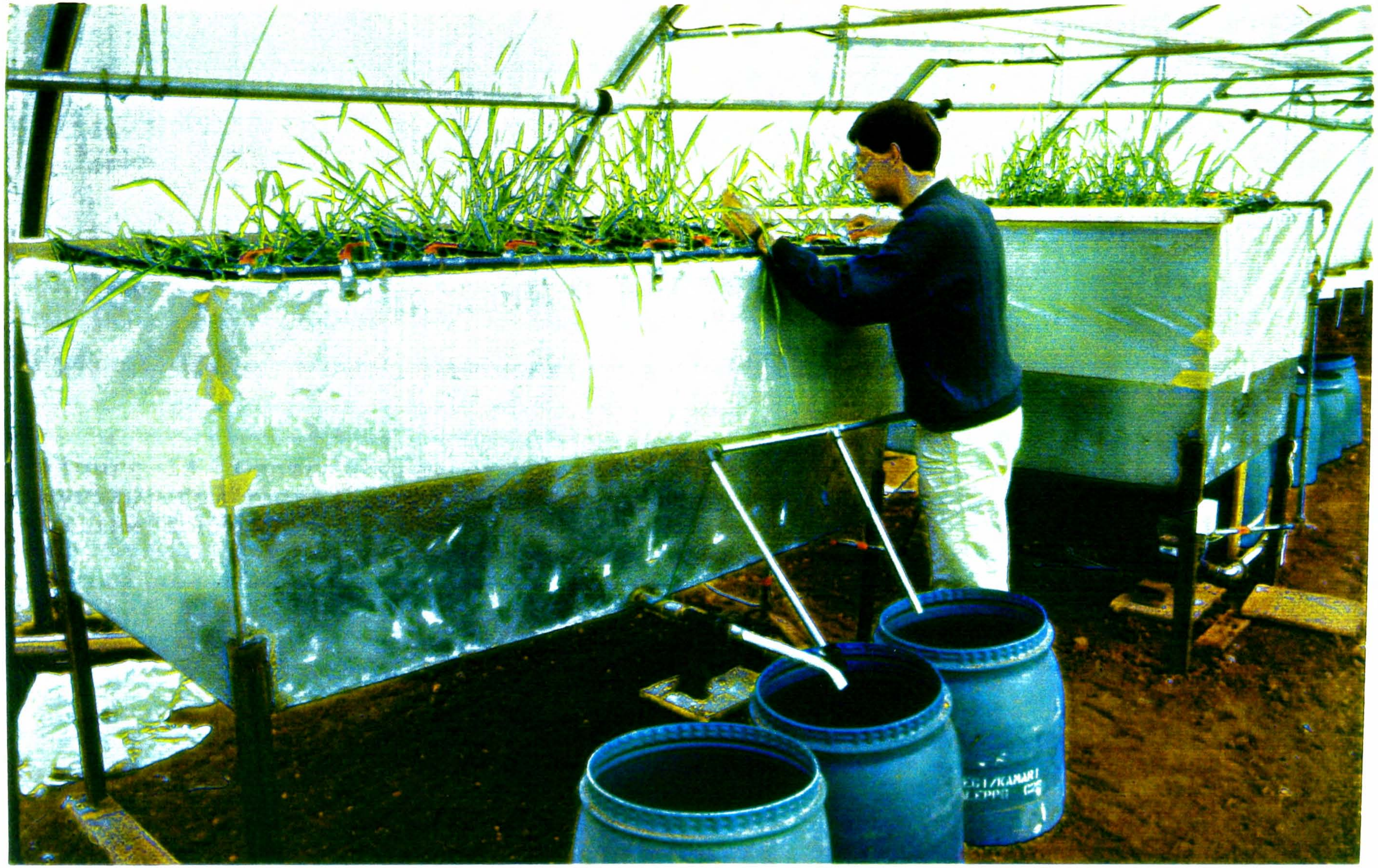

Figure 13. General view of the sand-culture apparatus used at Tel Hadya, Syria, for screening durum wheat genetic resources under controlled saline conditions.

Figure 14. Detail of the sand-culture apparatus used at Tel Hadya, Syria.

reached in treatments 2 and 3, one plant from each replication of each entry was harvested (early harvest). Length and width of the youngest, fully-expanded leaf was measured and, later, leaf area (LA) computed by the formula:

$$LA = \text{length} \times \text{width} \times 0.73$$

(Rawson *et al.*, 1988). Shoot fresh weight of the plant (FW) was recorded immediately after cutting, and dry weight (DW) after keeping the samples 24 hrs. in an oven at 105° C. Plant weight was used as a measure of stress tolerance. Rawson *et al.* (1988) stated that plant weight at harvest was the most realistic estimate of the already mentioned "absolute salinity tolerance", defined as the intrinsic high growth rate of the genotype. Results on plant weight of different genotypes in their experiment were comparable to previously documented responses to the stress by the same genotypes.

The remaining plants were grown under the same experimental regime until physiological maturity occurred (yellowed uppermost internode), that is, a maximum of about 180 days from sowing in the control, and 115 days in the treatment with 100 mol m^{-3} NaCl. None of the plants in the treatment with 200 mol m^{-3} NaCl survived to that stage. On all surviving plants in treatments 1 and 2 the following characters were recorded: number of days from sowing to heading (DHE); number of days from sowing to maturity (DMA); plant height (PLH); number of total tillers per plant (TOTIL); number of fertile tillers per plant (FETIL); number of leaves on the main stem (NOLV); leaf length and width of the flag leaf, leaf 2 and leaf 3; above-ground dry matter per plant (DM). The leaf area of the flag leaf (FLA), leaf 2 (LA2) and leaf 3 (LA3) was computed using the formula:

$$LA = \text{length} \times \text{width} \times 0.73 \, .$$

An analysis of variance (ANOVA) combining the factors 'entry' and 'salinity level' was carried out for the traits recorded during the early harvest, viz., leaf area, shoot fresh weight and dry weight. Variation among entries for these characters was tested at each salinity level and entry mean values were compared by the

Newman and Keuls test. Simple correlation coefficients among fresh weight, dry weight and leaf area entry mean values at the three salinity levels were computed.

A special emphasis was given in the statistical analysis of this experiment to five accessions which appeared rather different in response to the stress, and these were taken as possibly representative of the existing variability in the set of materials. The five entries were '5971', '17729', '4831', 'Sham 1' and 'S. Cappelli'. An ANOVA combining the factors 'entry' and 'salinity level' was performed for the three mentioned characters recorded during the early harvest. A mixed linear model was assumed in the ANOVA. 'Salinity level' was considered a fixed factor, that is, the salinity levels in the experiment were not randomly drawn from a population of possible treatments but were selected to represent a range of salt stress from absent to very severe. 'Entry' was treated as a random factor. Actually, the five entries tested were consciously selected and were not taken at random. However, given their diversified response to the stress, they were considered a random sample of a population of durum wheat genotypes evaluated for salt tolerance. The sum of squares and degrees of freedom of the factor 'salinity level' and of the interaction 'entry x salinity level' were partitioned to give an orthogonal set of comparisons (Steel and Torrie, 1960, chapter 11) which concerned salinity level mean values and salinity level interactions with entries, as shown later in Table 45. Given this model, the 'salinity level' mean square was tested on the 'entry x salinity level' interaction mean square, while all other tests were made against the error mean square (Dagnelie, 1975, chapter 15).

The ten morpho-physiological characters recorded during the second phase of the experiment on all 34 accessions were used in a combined ANOVA with the factors 'entry' and 'salinity level' (which, as already mentioned, was either the control or 100 mol m^{-3} NaCl, no plants having survived in the treatment with 200 mol m^{-3} NaCl). Variation among entries was tested in both salt treatments by ANOVA and entry mean values were compared by the Newman and Keuls test.

The ratios between the entry mean values at 100 mol m^{-3} NaCl and those in the control were computed for all traits. A simple correlation analysis assessed the relationships between the ratios for the various characters.

6.2.1.2 *Results and discussion*

The electrical conductivity (EC) measured in the drainage of the three tanks during the experiment varied between 1.07 and 1.25 dS m^{-1} (=mmho cm^{-1}) in the control; between 10.90 and 12.88 dS m^{-1} in the treatment with 100 mol m^{-3} NaCl; between 21.41 and 24.60 dS m^{-1} in the treatment with 200 mol m^{-3} NaCl.

Overall mean values for the traits recorded during the early harvest are shown in Table 40. It is evident that the overall effect of the treatment with 100 mol m^{-3} NaCl relative to the control was rather limited, except for the leaf area which was reduced by over 30%, on average, by this treatment. All characters were drastically reduced by the treatment with 200 mol m^{-3} NaCl, although variability of response was still present. The results of the combined ANOVA for these characters are reported in Table 41. The factors 'entry' and 'salinity level' were always highly significant, while the 'entry x salinity level' interaction for both fresh and dry shoot weight was not significant.

Entry differences for fresh weight, dry weight and leaf area tested at each salt content by ANOVA were always significant ($P < 0.05$) (data not shown). In order to examine the rank variation among salinity levels, entry mean values were compared by the Newman and Keuls test at each level. The best ranking entries for each trait at each level, not differing from each other according to the test, are listed in Table 42. The results highlighted the relative performance of '5971' across salinities, and especially at 200 mol m^{-3} NaCl. Other accessions worth of

Table 40. Overall mean value (± s.e.) of 34 durum wheat entries for shoot fresh weight, shoot dry weight and area of the youngest, fully-expanded leaf per plant at three salinity levels. Experiment Tel Hadya 1989, early harvest.

	control	100 mol m^{-3} NaCl	200 mol m^{-3} NaCl
Character	Mean	Mean	Mean
Shoot fresh weight (g)	4.81 ± 0.31	4.00 ± 0.29	1.29 ± 0.11
Shoot dry weight (g)	1.36 ± 0.10	1.17 ± 0.09	0.49 ± 0.04
Leaf area (cm^2)	17.04 ± 0.92	11.68 ± 0.56	4.41 ± 0.32

Table 41. Results of the combined analysis of variance on 34 durum wheat entries evaluated in the experiment Tel Hadya 1989, early harvest.

Source of variation			
	Shoot fresh weight		
	df	MS	F[a]
entry	33	21.9	7.38 ***
salinity level	2	517.9	135.91 ***
entry x salinity level	65	3.8	1.28 ns
error	377	2.9	
	Shoot dry weight		
	df	MS	F
entry	33	2.4	5.65 ***
salinity level	2	31.6	70.28 ***
entry x salinity level	65	0.4	1.08 ns
error	377	0.4	
	Leaf area		
	df	MS	F
entry	33	142.2	8.73 ***
salinity level	2	6051.0	196.09 ***
entry x salinity level	65	30.8	1.89 ***
error	377	16.3	

---

[a] ns, *, ***: not significant, significant at $P \leq 0.05$ and $P \leq 0.001$, respectively.

Table 42. Best ranking entries not differing from each other according to the Newman and Keuls test, for the characters shoot fresh weight (FW), shoot dry weight (DW) and area of the youngest, fully expanded leaf per plant (LA) at three salinity levels. Experiment Tel Hadya 1989, early harvest.

FW-con[a]	FW-100[b]	FW-200[c]	DW-con	DW-100	DW-200	LA-con	LA-100	LA-200
Cappelli	18376	5971	17329	18376	5971	8944	18376	5971
17329	Cappelli		5971	Cappelli		38552	5971	
5971	17729		Cappelli	17729		17329	17729	
	5971		18376	16447		Cappelli	5694	
	8907					5971	10115	
	17329					16420	8907	
	16447					6062	Cappelli	
	8944					17729	38552	
	16420					6582	16420	
							17329	
							16447	
							18038	
							8944	

[a] con: control
[b] 100: 100 mol m^{-3} NaCl
[c] 200: 200 mol m^{-3} NaCl

mention were 'S. Cappelli', '18376', '17329' and '8944', the means of which were in most cases among the highest at 100 mol m^{-3} NaCl and immediately following those of '5971' at 200 mol m^{-3} NaCl (data not shown). Entry '17729' had an interesting behaviour, appearing at the top for the three characters at 100 mol m^{-3} NaCl but dropping to an average position at 200 mol m^{-3} NaCl (data not shown).

Table 43 shows the simple correlation coefficients among shoot fresh weight, dry weight and leaf area entry mean values at the three salt contents. It is evident that the three characters were well correlated within each salt treatment as well as across salinity levels.

Mean values of fresh weight, dry weight and leaf area of the five entries which received particular attention in the analysis of the results are shown in Table 44. It appears that the responses of '4831' and 'Sham 1' were less affected across salinity levels than those of the three other accessions, especially in terms of shoot weight. However, at 100 mol m^{-3} NaCl external concentration the mean values of 'Sham 1' and, particularly, '4831' were lower than the others. 'S. Cappelli' and '17729' seemed little affected by the stress at 100 mol m^{-3} NaCl, while their values dropped sharply at 200 mol m^{-3} NaCl. The possible combination of high growth rate and little reduction at 100 mol m^{-3} NaCl relative to the control, which is suggested by the data of 'S. Cappelli' and '17729', would make these entries of some interest under conditions of moderately high salinity.

The results of the combined ANOVA performed on the five accessions are reported in Table 45. Entries differed highly for all traits; salt treatments were always significantly different, though at various probability levels. The control treatment was significantly different from the treatment with 100 mol m^{-3} NaCl only for the variable leaf area, while the latter treatment was always highly different from the treatment with 200 mol m^{-3} NaCl. The 'entry x salinity level' interaction was significant for all traits except dry weight. The interaction contrasts were

Table 43. Simple correlation coefficients among shoot fresh weight (FW), shoot dry weight (DW) and area of the youngest, fully-expanded leaf per plant (LA) at three salinity levels. Experiment Tel Hadya 1989, early harvest.

	FW-100	FW-200	DW-con	DW-100	DW-200	LA-con	LA-100	LA-200
FW-con[a]	0.85 ***	0.64 ***	0.95 ***	0.78 ***	0.55 ***	0.82 ***	0.79 ***	0.69 ***
FW-100[b]	-	0.62 ***	0.83 ***	0.97 ***	0.59 ***	0.71 ***	0.90 ***	0.66 ***
FW-200[c]		-	0.69 ***	0.63 ***	0.96 ***	0.40 *	0.49 **	0.75 ***
DW-con			-	0.78 ***	0.59 ***	0.73 ***	0.78 ***	0.69 ***
DW-100				-	0.63 ***	0.64 ***	0.84 ***	0.59 ***
DW-200					-	0.39 *	0.43 *	0.67 ***
LA-con						-	0.76 ***	0.64 ***
LA-100							-	0.70 ***

*, **, *** : significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively (N=34).

[a] con: control
[b] 100: 100 mol m^{-3} NaCl
[c] 200: 200 mol m^{-3} NaCl

Table 44. Shoot fresh weight (FW), shoot dry weight (DW) and area of the youngest, fully-expanded leaf per plant (LA) of five durum wheat entries at three salt external concentrations. Values are means of five replications ± standard error of means. Experiment Tel Hadya 1989, early harvest.

	control		
Entry	FW (g)	DW (g)	LA (cm^2)
4831	1.48±0.22	0.31±0.03	9.8±1.9
5971	7.53±1.25	2.50±0.54	22.4±2.9
17729	6.76±1.24	1.93±0.49	21.4±2.1
S. Cappelli	8.34±0.97	2.43±0.40	23.1±1.1
Sham 1	2.95±0.83	1.08±0.36	8.2±1.4

	100 mol m^{-3} NaCl		
Entry	FW (g)	DW (g)	LA (cm^2)
4831	1.52±0.28	0.39±0.08	6.5±1.2
5971	6.15±0.95	1.88±0.36	16.4±1.6
17729	6.37±1.33	2.02±0.45	16.2±2.0
S. Cappelli	6.85±1.35	2.32±0.62	15.2±1.8
Sham 1	3.51±0.81	1.21±0.29	9.4±1.1

	200 mol m^{-3} NaCl		
Entry	FW (g)	DW (g)	LA (cm^2)
4831	0.52±0.13	0.36±0.21	2.0±0.5
5971	3.45±0.10	1.25±0.31	10.4±1.8
17729	1.05±0.18	0.40±0.08	5.1±0.3
S. Cappelli	2.09±0.81	0.70±0.23	5.6±1.8
Sham 1	1.74±0.50	0.74±0.27	3.3±0.6

Table 45. Analysis of variance of five durum wheat entries for the traits shoot fresh weight (FW), shoot dry weight (DW) and area of the youngest, fully-expanded leaf per plant (LA). Experiment Tel Hadya 1989, early harvest.

		Mean square[b]		
Source of variation	df	FW	DW	LA
entry	4	59.5 ***	5.9 ***	333.6 ***
salinity level[a]	2	90.8 **	6.6 *	825.5 ***
- con vs. 100	1	3.5 ns	0.1 ns	223.4 ***
- 100 vs. 200	1	115.2 ***	9.1 ***	659.9 ***
entry x salinity level	8	8.4 *	1.0 ns	39.4 **
- entry x (con vs. 100)	4	2.0 ns	0.2 ns	29.6 ns
- entry x (100 vs. 200)	4	8.4 ns	1.2 ns	18.2 ns
error	58	3.8	0.6	13.1

[a] con: control; 100: 100 mol m^{-3} NaCl; 200: 200 mol m^{-3} NaCl.

[b] ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

not significant, indicating that the entry responses were the same to each pair of salt treatments.

The results of the ANOVA carried out on the morpho-agronomic characters recorded during the second phase of the experiment (final harvest) on 34 entries are reported in Table 46. Differences among entries were significant for all traits except number of fertile tillers. There were highly significant differences between salinity levels for all characters. 'Entry x salinity level' interaction was significant for all traits except plant height, number of fertile tillers and number of leaves on the main stem. The presence of this interaction was confirmed by the difference between entry ranks in the two treatments (data not shown). The F-test results of the ANOVA among entries for all traits in the two treatments are shown in Table 47. While the entries were significantly different for all characters in the control, these differences were not significant at 100 mol m^{-3} NaCl for the maturity date and for the number of both total and fertile tillers. Growth in 100 mol m^{-3} NaCl caused substantial changes in the plant response for all traits, as made evident by the treatment mean values reported in Table 47. At this salinity level, the plant cycle was shorter, especially the period between heading and maturity (grain filling). Rawson *et al.* (1988) found that phenological development was accelerated with increasing salinity. The plants under stress in the present study were shorter and with less tillers, but they had more leaves on the main stem. Leaf area was reduced for the three measured leaves, leaf 3 being the least affected. The reduction of dry matter per plant in the present experiment was outstanding, the mean at 100 mol m^{-3} NaCl being only 36% of that in the control. However, entry '3772' had a dry matter at 100 mol m^{-3} NaCl practically equal to that in the control, while entries '3989', '3125' and '18038' had dry matter ratios greater than 0.80, i.e., a reduction of less than 20% caused by the salinity stress. Entry '8944' had the greatest dry matter reduction and did not confirm in the final harvest the interesting behaviour previously reported for the early harvest.

Table 46. Summary of the analysis of variance for ten morpho-physiological traits recorded on 34 durum wheat entries at two salinity levels (control and 100 mol m^{-3} NaCl). Experiment Tel Hadya 1989, final harvest.

Source of variation	df	Mean square	df	Mean square
		Days to heading		No. leaves on main stem
entry	33	917.7 ***	33	3.24 ***
salinity level	1	13259.9 ***	1	87.37 ***
entry x salinity level	33	456.4 ***	33	0.98 ns
error	220	130.1	187	0.96
		Days to maturity		Flag-leaf area
entry	33	834.3 ***	33	152.3 ***
salinity level	1	49578.8 ***	1	3290.8 ***
entry x salinity level	33	679.6 *	33	71.0 **
error	132	350.3	187	37.8
		Plant height		2nd-leaf area
entry	33	1232.5 ***	33	107.6 ***
salinity level	1	9175.8 ***	1	2129.6 ***
entry x salinity level	33	193.1 ns	33	71.2 ***
error	186	170.0	185	22.7

(continued next page)

Table 46 (continued).

Source of variation	df	Mean square	df	Mean square
		No. total tillers		3rd-leaf area
entry	33	2.7 *	33	81.9 ***
salinity level	1	201.4 ***	1	649.9 **
entry x salinity level	33	3.5 ***	33	60.9 ***
error	187	1.6	186	17.9
		No. fertile tillers		Dry matter per plant
entry	33	1.3 ns	33	89.5 ***
salinity level	1	81.7 ***	1	2447.6 ***
entry x salinity level	33	1.3 ns	33	76.4 ***
error	187	0.9	187	20.3

ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 47. The effect of salinity (control and 100 mol m^{-3} NaCl) on various measured parameters on 34 durum wheat accessions, together with the ratio of the 100 mol m^{-3} treatment to the control. Values shown are means ± standard errors. Numbers in parentheses are the accessions with lowest and highest ratio values. Experiment Tel Hadya 1989, final harvest.

	control		100 mol m^{-3} NaCl		100 mol : control	
	Mean	F-test signif.[a]	Mean	F-test signif.[a]	Mean	
Days to heading	75.9 ± 3.0	***	62.7 ± 0.8	**	0.85 ± 0.03	(16566 3402)
Days to maturity	131.2 ± 3.7	***	89.8 ± 1.5	ns	0.71 ± 0.03	(5187 3989)
Plant height (cm)	67.1 ± 2.6	***	55.9 ± 2.2	***	0.80 ± 0.02	(5131 16447)
No. total tillers	3.6 ± 0.2	***	1.7 ± 0.1	ns	0.57 ± 0.06	(3157 5694)
No. fertile tillers	2.4 ± 0.1	*	1.2 ± 0.1	ns	0.56 ± 0.04	(3157 5694)
No. leaves on main stem	4.6 ± 0.1	**	6.1 ± 0.1	**	1.29 ± 0.03	(5694 16566)
Flag-leaf area (cm^2)	16.7 ± 1.2	***	8.8 ± 0.5	***	0.60 ± 0.04	(8944 6230)
2nd-leaf area (cm^2)	13.9 ± 1.1	***	7.7 ± 0.4	***	0.62 ± 0.04	(5187 3125)
3rd-leaf area (cm^2)	10.0 ± 1.0	***	6.6 ± 0.3	**	0.83 ± 0.08	(5187 3989)
Dry matter per plant (g)	29.01± 3.38	***	7.19± 0.51	***	0.36 ± 0.05	(8944 3772)

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[a] ns, *, **, *** : not significant, significant at P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001.

The ratios of the values of the ten recorded characters at 100 mol m^{-3} NaCl to those in the control were correlated among themselves (Table 48). The ratio of dry matter was positively correlated to those of heading and maturity date, number of tillers, and leaf area (the area of the third leaf being more important than the two other leaf areas). That is, the shorter the crop cycle, or the fewer the tillers, or the smaller the leaves at 100 mol m^{-3} NaCl relative to the control, the greater the reduction of biomass. The effect of the salt stress on maturity time (ratio-DMA) was correlated with the effect on the total number of tillers (ratio-TOTIL) and on the three measured leaf areas (ratio-FLA, ratio-LA2 and ratio-LA3). These latter ratios were closely and positively correlated to each other, which indicated that the stress acted in the same manner on all leaves.

Six entries tentatively classified as "tolerant" and six as "susceptible" on the basis of the field screening carried out at Hegla (section 6.1) were included in the experiment Tel Hadya 1989. The results for these two groups of accessions are shown in Table 49. Under artificially induced salt stress the two groups did not differ, on average, for any character recorded either in the early harvest or in the final harvest. It is worth mentioning that the effect of the salt stress on the recorded morpho-physiological traits was either highest or lowest for some of these entries compared to the other accessions (Table 47). However, this effect was not always the one expected on the basis of their previous response to field stress. For instance, entry '3157', which was tentatively classified as salt tolerant in the field, had the greatest reduction of tiller number at 100 mol m^{-3} NaCl relative to the control in the greenhouse. Entry '5131', which belonged to the "tolerant" group in the field, had the lowest plant height in the stress treatment relative to the control. Entry '3125', having been tentatively classified as "susceptible" in the field screening, had instead a good response for all characters in the salt treatment of the greenhouse experiment. Only two entries seemed to confirm in the present study the previous classification, viz., '5187' as possibly susceptible and '3772' as

Table 48. Matrix of the correlation coefficients among the ratios between the measurements at 100 mol NaCl and those in the control treatments for ten morpho-physiological traits recorded on 34 durum wh entries. For trait abbreviations see section 6.2.1.1. Experiment Tel Hadya 1989, final harvest.

	2	3	4	5	6	7	8	9	10
1) Ratio-DHE	0.73 ***	-0.37 *	0.40 *	ns	ns	ns	0.35 *	0.36 *	0.63
2) Ratio-DMA	-	ns	0.73 ***	ns	ns	0.57 **	0.49 **	0.70 ***	0.72
3) Ratio-PLH		-	ns	ns	0.47 **	ns	ns	ns	ns
4) Tatio-TOTIL			-	0.81 ***	-0.36 *	ns	ns	0.35 *	0.81
5) Ratio-FETIL				-	-0.35 *	ns	ns	0.35 *	0.60
6) Ratio-NOLV					-	ns	ns	ns	ns
7) Ratio-FLA						-	0.64 ***	0.56 ***	0.44
8) Ratio-LA2							-	0.80 ***	0.55
9) Ratio-LA3								-	0.70
10) Ratio-DM									-

ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 49. Comparison of the characters recorded under salt stress both in the early harvest (A) and in the final harvest (B) (experiment Tel Hadya 1989) between the two groups of accessions tentatively classified as salt "tolerant" and "susceptible" on the basis of a field screening carried out under naturally occurring strss. For trait abbreviations see section 6.2.1.1.

A)

	100 mol m^{-3} NaCl			200 mol m^{-3} NaCl		
	FW (g)	DW (g)	LA (cm^2)	FW (g)	DW (g)	LA (cm^2)
Tolerant	2.5	0.7	8.5	1.0	0.4	3.5
Susceptible	2.9	0.8	9.5	0.9	0.3	2.7

B)

	100 mol m^{-3} NaCl									
	DHE (dd.)	DMA (dd.)	PLH (cm)	TOTIL (no.)	FETIL (no.)	NOLV (no.)	FLA (cm^2)	LA2 (cm^2)	LA3 (cm^2)	DM (g)
Tolerant	62.5	90.4	48.3	1.8	1.3	5.8	7.9	6.8	5.8	5.8
Susceptible	64.1	89.0	54.0	1.7	1.1	6.3	6.9	5.7	6.0	5.3

Mean values of the two groups in each variable are not different at $P \leq 0.05$ according to t-test.

possibly tolerant. The stability of response of the latter accession was remarkable and was also confirmed by the results of the early harvest (data not shown) where the values of shoot fresh weight, dry weight and leaf area were almost the same in the control and at 100 mol m^{-3} NaCl, while they dropped at 200 mol m^{-3} NaCl.

6.2.2 *Experiment Tel Hadya 1990*

6.2.2.1 *Materials and methods*

A second experiment was carried out at Tel Hadya in late spring-early summer 1990, using the same greenhouse facilities described in section 6.2.1.1. This trial included the five durum wheat accessions which were examined in detail in 1989 (viz., '4831', '5971', '17729', 'Sham 1' and 'S. Cappelli'), together with two entries ('19606' and '38584') which were chosen on the basis of promising results in one experiment carried out at Bangor (section 7.1.2). The three treatments in the present experiment included a control, 50 mol m^{-3} NaCl and 100 mol m^{-3} NaCl. In each treatment a randomised complete block design with 15 replications was adopted, each entry being represented in each replication by a single seedling. The seeds were sown, 10 cm apart from each side, in the second half of May. The salt was added to the nutrient solution starting a week later and increasing by 25 mol m^{-3} day^{-1} until the required salinity was reached. $CaCl_2$ was added as in the previous experiment to maintain a nominal Na:Ca ratio of 20:1. Five weeks from germination, and after four weeks at full salinity, all plants were harvested in the three treatments. Shoot fresh weight (FW) and green fresh weight (GFW) (i.e., shoot fresh weight after removing all necrotic areas of the leaves) were recorded for each plant immediately after harvesting. Necrotic areas of the leaves were likely due to the effect of the stress. The FW/GFW ratio was calculated to give a measure of the extent of such an effect on each plot: the more necrotic areas were present on the leaves, the more the ratio exceeded the value of 1.

An ANOVA combining the factors 'entry' and 'salinity level', and including contrasts between salinity levels, was performed for the traits fresh weight and green fresh weight. The model was as the one described in section 6.2.1.1 for Tel Hadya 1989. Mean squares were tested as already described for Tel Hadya 1989. The differences among entries at each salinity level for shoot fresh weight, green fresh weight and the ratio between weights were tested by ANOVA, and entry means were compared by Duncan's multiple range test. The effect of the highest salinity level (100 mol m^{-3} NaCl) relative to the control treatment was assessed by computing the ratio between the entry mean values at 100 mol m^{-3} NaCl and those in the control.

6.2.2.2 *Results and discussion*

The electrical conductivity (EC) measured in the drainage of the three tanks during the experiment varied between 1.1 and 1.3 dS m^{-1} in the control, between 7.8 and 8.0 dS m^{-1} in the treatment with 50 mol m^{-3} NaCl, and between 11.1 and 12.4 dS m^{-1} in the treatment with 100 mol m^{-3} NaCl.

Mean values for shoot fresh weight, green fresh weight and weight ratio of the seven accessions used in this experiment are shown in Table 50. The seven entries differed significantly ($P \leq 0.001$) for fresh weight and green fresh weight at each salinity level. Differences were significant ($P \leq 0.05$) for FW/GFW ratio at 50 mol m^{-3} and 100 mol m^{-3} NaCl. Entries '4831' and 'Sham 1' confirmed the

Table 50. Shoot fresh weight (FW), green fresh weight (GFW) and FW/GFW ratio (RATIO) of seven durum wheat entries at three salt external concentrations. Values are means of 15 replications ± standard error of means. Experiment Tel Hadya 1990.

control

Entry	FW (g)	GFW(g)	RATIO
4831	1.72 ± 0.28 c	1.67 ± 0.28 c	1.04 ± 0.02 a
5971	2.98 ± 0.55 bc	2.92 ± 0.55 bc	1.03 ± 0.01 a
17729	3.01 ± 0.37 bc	2.98 ± 0.37 bc	1.01 ± 0.01 a
19606	2.96 ± 0.32 bc	2.90 ± 0.31 bc	1.02 ± 0.01 a
38584	4.66 ± 0.48 a	4.59 ± 0.48 a	1.01 ± 0.01 a
S. Cappelli	3.38 ± 0.54 ab	3.33 ± 0.54 ab	1.02 ± 0.01 a
Sham 1	1.61 ± 0.34 c	1.57 ± 0.34 c	1.05 ± 0.03 a

50 mol m^{-3} NaCl

Entry	FW (g)	GFW(g)	RATIO
4831	1.29 ± 0.23 b	1.20 ± 0.22 b	1.08 ± 0.01 b
5971	1.16 ± 0.50 b	1.08 ± 0.48 b	1.10 ± 0.03 b
17729	1.48 ± 0.76 b	1.32 ± 0.68 b	1.19 ± 0.10 a
19606	3.35 ± 0.49 a	3.20 ± 0.49 a	1.05 ± 0.01 b
38584	3.30 ± 0.60 a	3.15 ± 0.58 a	1.06 ± 0.01 b
S. Cappelli	2.07 ± 0.74 ab	1.93 ± 0.69 ab	1.08 ± 0.02 b
Sham 1	1.36 ± 0.19 b	1.28 ± 0.18 b	1.06 ± 0.01 b

100 mol m^{-3} NaCl

Entry	FW (g)	GFW(g)	RATIO
4831	1.21 ± 0.14 cd	1.08 ± 0.14 de	1.14 ± 0.02 a
5971	1.77 ± 0.23 bc	1.60 ± 0.22 cd	1.12 ± 0.02 ab
17729	1.74 ± 0.29 bc	1.55 ± 0.28 cd	1.17 ± 0.03 a
19606	2.96 ± 0.27 a	2.83 ± 0.26 a	1.05 ± 0.01 b
38584	2.71 ± 0.34 a	2.46 ± 0.32 ab	1.12 ± 0.02 ab
S. Cappelli	2.34 ± 0.29 ab	2.04 ± 0.27 bc	1.16 ± 0.03 a
Sham 1	0.90 ± 0.10 d	0.81 ± 0.10 e	1.16 ± 0.05 a

Mean values for each variable in each treatment followed by the same letter are not different at $P \leq 0.05$ according to Duncan's multiple range test.

low, intrinsic growth potential which they had shown in the previous experiment at Tel Hadya. '4831' was relatively less affected than other accessions at 100 mol m^{-3} NaCl as compared with the control treatment (Table 51). Of the other three accessions previously evaluated at Tel Hadya ('5971', '17729' and 'S. Cappelli') the former two did not seem to confirm the interesting response of the previous experiment. In the present evaluation '5971' did not have a high shoot weight across salinity levels (Table 50) as in Tel Hadya 1989, while '17729' was more affected at 100 mol m^{-3} NaCl relative to the control than in 1989 (Table 51). 'S. Cappelli' was not significantly different from the best ranking entries for fresh weight at 100 mol m^{-3} NaCl (Table 50) and had one of the least reductions of weight at this salt content relative to the control (Table 51). Some of the entries had a lower shoot weight at 50 mol m^{-3} NaCl than at 100 mol m^{-3} NaCl (Table 50). This result is difficult to explain by just a salt effect, and the former treatment appeared patchily affected by a possible pathogen attack. It is noteworthy that the two accessions not included in the experiment Tel Hadya 1989 and added to Tel Hadya 1990 on the basis of the results obtained at Bangor (viz., entries '19606' and '38584') ranked best for aerial biomass across salt contents (Table 50). '19606' had an outstandingly stable response in terms of shoot weight (Table 51) and a remarkably low FW/GFW ratio across salt contents, particularly at 100 mol m^{-3} NaCl where it had the lowest mean value (Tables 50 and 51). This entry seemed worth considering for possible further investigations, given its interesting features shown in this experiment.

The results of the combined ANOVA performed on the character fresh weight are reported in Table 52. Differences among entries and among salinity levels were highly significant. The control treatment was significantly different from the treatment with 50 mol m^{-3} NaCl, while the treatments with 50 mol m^{-3} NaCl and 100 mol m^{-3} NaCl were not different. The 'entry x salinity level' interaction was significant at $P \leq 0.05$, confirming the results obtained in the previous

Table 51. Ratio of the 100 mol m^{-3} NaCl treatment to the control treatment for the characters shoot fresh weight (FW), green fresh weight (GFW) and FW/GFW ratio (RATIO) recorded on seven durum wheat entries. Experiment Tel Hadya 1990.

Entry	FW	GFW	RATIO
4831	0.70	0.65	1.10
5971	0.59	0.55	1.09
17729	0.58	0.52	1.16
19606	1.00	0.97	1.03
38584	0.58	0.53	1.11
S. Cappelli	0.69	0.61	1.14
Sham 1	0.56	0.51	1.10
Mean	0.67	0.62	1.10
s.e.	0.06	0.06	0.01

Table 52. Analysis of variance of seven durum wheat entries for the character shoot fresh weight. Experiment Tel Hadya 1990.

Source of variation	df	MS	F
Entry	6	22.9	16.02 ***
Salinity level[a]	2	32.7	12.60 **
- con vs. 50	1	57.6	40.33 ***
- 50 vs. 100	1	3.3	2.30 ns
Entry x salinity level	12	2.6	1.82 *
- entry x (con vs. 50)	6	4.4	3.06 **
- entry x (50 vs. 100)	6	0.9	0.61 ns
Error	227	1.4	

[a] con: control; 50: 50 mol m^{-3} NaCl; 100: 100 mol m^{-3} NaCl.

ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

experiment where a relatively weak interaction between the entries and the salt treatments was found. Entries interacted in different ways to the control treatment in comparison with the treatment with 50 mol m^{-3} NaCl, while their response was not significantly different at 50 mol m^{-3} and 100 mol m^{-3} NaCl (Table 52).

6.2.3 *Salinity resistance in genetic resources of wild* Triticum *species. Experiment Tel Hadya—wild*

6.2.3.1 *Materials and methods*

For this study, five single spike progenies of *Triticum boeoticum* samples ($2n=2x=14$), and five of *T. dicoccoides* ($2n=2x=28$), all collected in Syria, were randomly selected from the wild wheat collection at the Genetic Resources Unit of ICARDA. Two wheat cultivars, namely the tetraploid durum wheat 'S. Cappelli' and the hexaploid bread wheat 'Mexipak' (= '7 Cerros'), were included as check entries. The trial was carried out using the same apparatus described in section 6.2.1.1. Three salt treatments were used: a control, 100 mol m^{-3} NaCl, and 150 mol m^{-3} NaCl. The salt was added to the nutrient solution starting on the 14th day after germination, when the seedlings were well established, and increased by 25 mol m^{-3} per day until the required salinity had been reached. $CaCl_2$ was added to the second and third treatment to maintain a nominal Na:Ca ratio of 20:1. Seeds of the 12 entries were sown in each tank (=treatment) in a randomised complete block design with eight replications, each replication of a line being represented by a single seedling. The resulting plants were 10 cm apart. Sowing took place at the beginning of November and the experiment spanned a 4-month period, the plants being harvested at the end of February. The following observations were recorded at the end of the cycle on each surviving plant: number of tillers per plant, number of leaves on the main tiller, number of days from germination to heading, peduncle length (cm), plant height (cm), number of spikes per plant and number of spikelets per spike. Given the high plant mortality observed in the treatment with 150 mol m^{-3} NaCl, the percentage surviving plants per entry in this treatment was also calculated.

A mixed-model analysis of variance (ANOVA) was carried out for each character, including the factors 'species', 'entry (species)', 'salinity level' and 'block'. 'Species' and 'salinity level' were considered fixed factors, while 'entry (species)' and 'block' were considered random. The experiment was analysed as a split-plot design (Steel and Torrie, 1960, chapter 12), with 'salinity level' on the main plot and 'entry (species)' on sub-plots. 'Salinity level' was tested on its interaction with the random factor 'entry (species)', while 'entry (species)', 'salinity level x species' and 'entry (species) x salinity level' were tested on the residual (Error B). 'Species' was tested on the random factor 'entry (species)'. The scheme of this analysis is shown in Table 53. Owing to plant mortality in the third treatment, only the control and the 100 mol m^{-3} NaCl level were included in the factor 'salinity level'. For the two wild species, as well as for the check cultivars, mean values at the two salinity levels were compared by ANOVA. Entry means within species were compared at each level by Duncan's multiple range test. The effect of salinity on each character was measured for each line as the ratio between the average value recorded at 100 mol m^{-3} NaCl and the average value in the control treatment. Entry ratios were averaged within species and wild species mean ratios were compared by a t-test. Similarly, for the lines which survived at 150 mol m^{-3} NaCl the ratio between the average values at this salinity level and the average values in the control were computed.

Table 53. Scheme of the analysis of variance performed on seven morphological traits. Experiment Tel Hadya-wild.

Source of variation	df
Species	1
Entry (species)	8 (4)[a]
Salinity level	1
Block	7
Species x salinity level	1
Entry (species) x salinity level	8 (4)
Error A	7
Error B	126 (70)

[a] in parentheses: number of degrees of freedom for the characters days to heading, peduncle length, plant height, number of spikes per plant, and number of spikelets per spike. The other degrees of freedom refer to the characters number of tillers per plant and number of leaves on the main stem.

6.2.3.2 *Results and discussion*

The percentage of surviving plants at 150 mol m^{-3} NaCl of each entry are reported in Table 54. None of the diploid entries or 'S. Cappelli' had living plants in this treatment at the end of the experiment, whereas all the 'Mexipak' plants survived this high artificially induced salinity stress. The lines of *T. dicoccoides* did not behave uniformly. While 'DICSNS165' and 'DICSNS173' had little or no survival, 'DICSNS157', 'DICSNS197' and 'DICSNS410' had plants living at 150 mol m^{-3} NaCl. For all check and wild wheat entries (also including those not heading) plant survival in the control treatment and at 100 mol m^{-3} NaCl was 100%.

Four lines, namely 'BONSN160', 'DICSNS165', 'DICSNS173' and 'DICSNS410', did not head at any salinity level, probably because insufficient vernalization occurred in the greenhouse (seeds were not vernalized prior to sowing). Therefore, all further analyses involving plant characters recorded from heading time onwards (i.e., days to heading, peduncle length, plant height, number of spikes per plant and number of spikelets per spike) will not include those four entries.

The results of the combined ANOVA are summarised in Table 55. Differences between species proved significant for all traits except number of tillers per plant and days to heading. Differences among entries were significant for all characters except number of spikelets per spike. Means of the two salinity levels (control and 100 mol m^{-3} NaCl) differed for number of leaves on the main tiller, peduncle length, plant height and number of spikelets per spike. 'Salinity level x species' interaction was significant ($P \leq 0.05$) only for plant height. None of the interactions 'entry (species) x salinity level' was significant. This latter result, if confirmed with a larger number of entries, would suggest the possibility of selec-

Table 54. Percent surviving plants of each entry at 150 mol m^{-3} NaCl external concentration. Experiment Tel Hadya-wild.

Entry	*Triticum* species	Ploidy	% surviving plants
BONSN135	*boeoticum*	2X	0
BONSN140	*boeoticum*	2X	0
BONSN160	*boeoticum*	2X	0
BONSN204	*boeoticum*	2X	0
BONSN296	*boeoticum*	2X	0
DICSNS157	*dicoccoides*	4X	100
DICSNS165	*dicoccoides*	4X	12.5
DICSNS173	*dicoccoides*	4X	0
DICSNS197	*dicoccoides*	4X	100
DICSNS410	*dicoccoides*	4X	100
S. Cappelli	*durum*	4X	0
Mexipak	*aestivum*	6X	100

Table 55. Mean squares of the main sources of variation from the ANOVA on seven morphological trait the scheme of which is shown in Table 53. Experiment Tel Hadya-wild.

Source of of variation	Mean squares						
	No. tillers per plant	No. leaves on main stem	Days to heading	Peduncle length	Plant height	No. spikes per plant	No. spikelet per spike
Species	213.9 ns	70.2 **	441.0 ns	16999.0 *	96939.2 **	106.5 *	135.0 **
Entry (species)	332.8 ***	5.6 ***	155.6 ***	2434.1 ***	1784.5 ***	10.9 ***	4.8 ns
Salinity level	49.5 ns	4.9 *	30.4 ns	115.7 ***	548.6 *	0.4 ns	55.5 *
Species x salinity level	88.5 ns	0.6 ns	0.1 ns	26.7 ns	131.7 *	0.4 ns	0.2 ns
Entry (species) x salinity level	24.8 ns	0.8 ns	4.4 ns	0.6 ns	29.0 ns	0.3 ns	3.5 ns

ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

ting wild wheat entries for salt tolerance (measured in terms of morphological traits) even in the absence of stress.

Entry and species mean values at both salinity levels of the recorded characters are shown in Table 56. In *T. boeoticum* the salt stress hastened the heading time, reduced the total stature, the length of the last internode and the number of spikelets per spike. None of the characters was significantly affected by the stress in *T. dicoccoides*. As regards the check cultivars, 'S. Cappelli' was affected in terms of number of tillers, plant height, peduncle length and number of spikes per plant, while 'Mexipak' showed a significant reduction at 100 mol m^{-3} NaCl only for the latter character. It is evident that, despite the same ploidy level, *T. dicoccoides* lines were, on average, less affected than 'S. Cappelli' in terms of morphological traits.

The absence of significant interactions between species and salinity as well as between entries and salinity is confirmed by the mean values shown in Table 56. Differences between wild species appeared consistent across salinity levels. At the same time there was little change in entry ranking between the control and the treatment with 100 mol m^{-3} NaCl.

The effect of the salt treatment on the different traits varied little among individual lines within both wild wheat species (Table 57). Only for number of tillers per plant was there variation among entries. The lines 'DICSNS410' and 'DICSNS197' showed a considerable increase in number of tillers in the salt treatment compared to the control. The two wild species differed for the response to salinity of peduncle length and plant height, *T. boeoticum* having a greater average reduction at 100 mol m^{-3} NaCl than *T. dicoccoides* for both characters. In both species the effect of salinity on number of tillers and on number of spikes per plant was much smaller than in the two check cultivars which had a reduction of about one third of tillers and spikes.

The effect of the highest salinity level relative to the control treatment was

Table 57. Effect of salinity on seven morphological characters, expressed as the ratio between the average values at 100 mol m^{-3} NaCl and the average values in the control treatment. Experiment Tel Hadya-wild.

Entry	Species[1]	No. of tillers	No. of leaves	Days to heading	Peduncle length	Plant height	No. of spikes	No. of spikelets
BONSN135	b	1.13	0.90	0.99	0.69	0.74	1.00	0.89
BONSN140	b	0.89	1.03	0.99	0.70	0.84	1.00	0.87
BONSN160	b	0.75	1.06	-	-	-	-	-
BONSN204	b	0.94	0.96	0.99	0.64	0.80	0.87	0.90
BONSN296	b	1.15	0.90	0.99	0.66	0.73	0.71	0.76
DICSNS157	ds	0.89	0.87	1.00	0.92	0.88	1.02	0.82
DICSNS165	ds	1.10	0.97	-	-	-	-	-
DICSNS173	ds	1.19	0.94	-	-	-	-	-
DICSNS197	ds	1.27	0.94	0.98	0.80	0.93	1.00	0.97
DICSNS410	ds	1.30	0.99	-	-	-	-	-
Mean *T. boeoticum*[2]		0.97 a	0.97 a	0.99 a	0.67 b	0.78 b	0.89 a	0.85 a
Mean *T. dicoccoides*[2]		1.15 a	0.94 a	0.99 a	0.86 a	0.90 a	1.01 a	0.89 a
S. Cappelli	d	0.60	0.99	1.04	0.84	0.82	0.68	0.86
Mexipak	ae	0.65	1.10	0.93	0.94	0.94	0.55	0.94

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[1] b: *Triticum boeoticum*; ds: *T. dicoccoides*; d: *T. durum*; ae: *T. aestivum*.
[2] In each character, wild species means followed by the same letter are not different according to t-test.

measured on the accessions surviving at 150 mol m^{-3} NaCl (Table 58). The *T. dicoccoides* lines 'DICSNS197' and 'DICSNS410' showed a much smaller reduction in tiller number under stress than the hexaploid cultivar 'Mexipak'. In the case of 'DICSNS157' the number of tillers even increased at 150 mol m^{-3} NaCl relative to the control treatment. The three *T. dicoccoides* lines had a similar response for the number of leaves on the main stem. While in the wild wheat entries this number decreased under stress, in 'Mexipak' it increased at 150 mol m^{-3} NaCl as it tended to increase also at 100 mol m^{-3} NaCl external concentration. The two tetraploid entries able to flower had a ratio for heading time, number of spikes per plant and number of spikelets per spike rather similar to that of 'Mexipak', and a markedly lower ratio for peduncle length and plant height compared with the hexaploid cultivar. For the two latter traits 'DICSNS197' was, however, less affected by high salinity than 'DICSNS157'.

Although based on a limited number of accessions, some inferences could be drawn from the present study. In spite of the absence of the enhanced K/Na discrimination trait in the tetraploid species (see section 1.3), *T. dicoccoides* seemed to have a better ability to grow under saline conditions than *T. boeoticum*. At 100 mol m^{-3} NaCl the former entries were less affected in general, while at the higher stress level a great variability of behaviour was observed in the tetraploid wild species. The three lines of *T. dicoccoides* which survived until the end of the cycle had better tolerance than the durum wheat cultivar 'S. Cappelli'. The different response to salinity between tetraploid species, as well as the variability within *T. dicoccoides* suggest the need of further investigation of larger collections of genetic resources of wild tetraploid wheats, in search of genotypes which may be used to improve the salt tolerance of the related durum wheat.

Table 58. Effect of salinity on seven morphological characters, expressed as the ratio between the average values at 150 mol m^{-3} NaCl and the average values in the control treatment. Experiment Tel Hadya-wild.

Entry	Number of tillers	Number of leaves	Days to heading	Peduncle length	Plant height	Number of spikes	Number of spikelets
DICSNS157	2.17	0.88	1.06	0.17	0.39	0.65	0.76
DICSNS197	0.78	0.78	0.98	0.58	0.66	0.54	0.89
DICSNS410	0.80	0.82	-	-	-	-	-
Mexipak	0.49	1.19	1.03	0.88	0.87	0.44	0.91

7 *Salinity experiments in Bangor*

7.1 *Greenhouse assessment of salinity resistance with hydroponics technique*

Two greenhouse experiments were carried out at Bangor during 1990. The aim of these experiments was to evaluate for salt tolerance during the early stages of development some durum wheat accessions from the ICARDA collection. In these experiments plants were grown in hydroponics instead of in a sand substratum as used for the experiments in Syria (section 6.2). Since in glycophytes, and especially in members of the *Gramineae*, salt tolerance is mainly associated with the ability to limit the accumulation of Na and Cl and with the maintenance of a high K/Na ratio (Greenway and Munns, 1980; Gorham *et al.*, 1985a), ion accumulation has also been examined in these experiments.

7.1.1 *Experiment Bangor 1990*

The five durum wheat entries ('4831', '5971', '17729' 'Sham 1' and 'S. Cappelli') given special emphasis in the assessment of salinity resistance in sand-culture experiments (section 6.2) were also evaluated in saline hydroponic-culture, using the facilities available at the Centre for Arid Zone Studies, Bangor. Seeds of the five entries were soaked overnight and then sown in rockwool plugs in P180 plug-trays with one seed per cell. In each tray (=treatment), nine replications per entry, each consisting of one plant, were placed in a randomised complete block design. The seeds were germinated at 25° C in the dark with the plug-trays placed over vermiculite moistened with a solution containing 2 mol m^{-3} $Ca(NO_3)_2$ and 1 mol m^{-3} $MgSO_4$. After five days the trays were suspended over 25 dm^3 of aerated "Phostrogen"-based nutrient solution (Gorham *et al.*, 1984). The plants were grown during January-February in a greenhouse with a minimum temperature of about 15° C and a photoperiod of 16 hrs. consisting of natural light supplemented with 400 W Son-T sodium vapour lamps. The nutrient solution was replaced every 10 days. Four salt treatments (containing respectively 50, 100, 150 and 200 mol m^{-3} NaCl) and a control were used. Salt was added to the nutrient solution starting 14 days after germination and increasing by 50 mol m^{-3} day^{-1} until the required salinity had been reached. $CaCl_2$ was added to maintain a nominal Na:Ca ratio of 20:1. The salt was added *via* a 0.9 mm internal diameter polythene tube which discharged the salt into an air-lift, where it was mixed with the bulk of the nutrient solution. This procedure avoided disturbance to the roots during addition of salt (Gorham, 1990).

All plants of each accession in each treatment were harvested after four weeks at the specified salinity level. Shoot fresh weight (FW) and green fresh weight (GFW) (i.e., fresh weight after removing all necrotic areas of the leaves) were recorded immediately after harvesting. The FW/GFW ratio was calculated, as in the experiment Tel Hadya 1990 (section 6.2.2.1). The youngest, fully-expanded leaf of each plant (=replication) in each accession was placed in a microcentrifuge tube and frozen. After thawing the tissue and expressing the sap, the sap and the tissue were separated by centrifugation at 5000 g for five minutes. The centrifuged extract was diluted (20 μl sap : 5 ml H_2O = 1 : 250) and used for the determination of various ions. Inorganic ion analysis was performed by ion chromatography using a Dionex 2010i ion chromatograph according to the procedure described by Gorham (1987). In this way, sodium, potassium, chloride, nitrate, orthophosphate and sulphate ions were determined (mol m^{-3} expressed sap). Sap osmotic potential (OP) was measured (mOsmol kg^{-1}) by a Wescor 5100B vapour osmometer.

The data recorded for shoot fresh weight, green fresh weight and their ratio were subject to ANOVA with the factors 'salinity level', 'entry' and 'block'. The variance of 'salinity level' (assumed to be a fixed factor) was tested on the variance of its interaction with 'entry' (considered random). The variance of 'entry' and of the interaction 'entry x salinity level' were tested on the error variance. An ANOVA tested entry differences for all recorded characters at each salinity level, and entry mean values were compared by Duncan's multiple range test. Salinity level mean values were compared by Duncan's multiple range test.

Mean values for shoot fresh weight, green fresh weight, their ratio and osmotic potential of the five entries are reported in Table 59. The mean values for the measured cation concentrations are shown in Table 60, while Table 61 reports the anion mean values. The results show that little differences occurred among the five tested entries at the various salinity concentrations. The F-test for fresh weight and green fresh weight was just significant at $P \leq 0.10$ at 50, 150 and 200 mol m^{-3} NaCl and the entry mean separation was never clear-cut. The entries never differed for Na^+ content and for sap osmotic potential. There were significant differences among entries in terms of K^+ content, K/Na ratio and Cl^- content only at 50 mol m^{-3} external concentration. Differences for PO_4^{3-} content were significant at all salinity levels except the highest, with '4831' showing, in general, the lowest values. This entry had also a general, remarkably higher content of SO_4^{2-} than the other accessions. Not enough green matter could be sampled from 'Sham 1' at 200 mol m^{-3} NaCl to determine the ion concentrations and the osmotic potential.

There appeared to be competition for uptake between the two monovalent anions (Cl^- and NO_3^-). On increasing the concentration of Cl^- the content of NO_3^- markedly decreased. That Cl^- inhibits NO_3^- uptake has been observed in several

Table 59. Mean values (± s.e.) of shoot fresh weight (FW), green fresh weight (GFW), FW/GFW ratio (RATIO) and osmotic potential (OP) of five durum wheat entries at five salt external concentrations. Experiment Bangor 1990.

	control				50 mol m^{-3} NaCl			
Entry	FW (g)	GFW(g)	RATIO	OP (mOsmol kg^{-1})	FW (g)	GFW(g)	RATIO	OP (mOsmol kg^{-1})
4831	4.90±0.75	4.84±0.75	1.01±0.01	427.1±8.3	3.02±0.28	2.92±0.27	1.03±0.01	586.7±17.0
5971	3.98±0.59	3.78±0.61	1.06±0.02	457.8±30.7	1.51±0.40	1.42±0.39	1.08±0.03	679.0±51.7
17729	2.91±0.33	2.81±0.34	1.04±0.01	451.0±10.1	2.05±0.64	1.88±0.62	1.20±0.12	717.0±157.0
S. Cappelli	3.70±0.74	3.56±0.73	1.05±0.01	466.1±28.1	2.10±0.60	1.91±0.57	1.11±0.02	620.5±39.5
Sham 1	2.57±0.61	2.51±0.60	1.02±0.01	556.0±119.8	1.94±0.26	1.86±0.25	1.04±0.01	578.9±28.9

	100 mol m^{-3} NaCl				150 mol m^{-3} NaCl			
Entry	FW (g)	GFW(g)	RATIO	OP (mOsmol kg^{-1})	FW (g)	GFW(g)	RATIO	OP (mOsmol kg^{-1})
4831	1.33±0.21	1.22±0.20	1.10±0.02	739.3±39.8	0.70±0.12	0.55±0.12	1.99±0.52	1007.4±199.8
5971	1.07±0.27	0.87±0.28	1.17±0.04	929.4±116.9	0.78±0.21	0.68±0.19	1.21±0.05	823.0±51.4
17729	1.32±0.34	1.21±0.32	1.11±0.02	744.6±42.7	0.89±0.17	0.77±0.16	1.17±0.03	853.2±39.7
S. Cappelli	1.83±0.37	1.61±0.37	1.30±0.22	868.7±75.5	0.63±0.08	0.47±0.09	1.49±0.13	1110.2±296.8
Sham 1	1.01±0.21	0.88±0.21	1.15±0.03	949.7±100.1	0.40±0.05	0.27±0.05	1.43±0.07	1450.0±375.0

	200 mol m^{-3} NaCl			
Entry	FW (g)	GFW(g)	RATIO	OP (mOsmol kg^{-1})
4831	0.69±0.13	0.55±0.13	1.30±0.08	1087.8±42.8
5971	0.57±0.19	0.48±0.18	1.35±0.12	1246.3±200.6
17729	0.66±0.15	0.53±0.13	1.29±0.07	1585.3±186.2
S. Cappelli	0.64±0.18	0.49±0.16	1.41±0.13	959.7±123.7
Sham 1[a]	0.24±0.04	0.13±0.04	1.67±0.13	-

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[a] not enough green material to make the missing measurement.

Table 60. Mean values (± s.e.) of sodium (Na^+) and potassium (K^+) ion concentration (mol m^{-3} expressed sap) and their ratio (K/Na) of five durum wheat entries at five salt external concentrations. Experiment Bangor 1990.

	control			50 mol m^{-3} NaCl		
Entry	Na^+	K^+	K/Na	Na^+	K^+	K/Na
4831	9.8±2.6	238.3±10.2	30.6±4.3	262.4±18.0	64.1±10.1	0.26±0.05
5971	8.5±0.6	268.0±9.8	32.2±2.2	302.3±23.1	72.3±16.6	0.26±0.07
17729	12.0±3.8	266.2±9.5	27.4±5.9	226.0±23.6	117.0±9.2	0.54±0.09
S. Cappelli	11.3±1.7	233.3±12.4	23.0±2.9	296.7±17.0	85.5±8.6	0.29±0.03
Sham 1	12.2±3.4	224.8±6.6	24.4±5.4	270.1±14.6	53.1±5.1	0.20±0.03

	100 mol m^{-3} NaCl			150 mol m^{-3} NaCl		
Entry	Na^+	K^+	K/Na	Na^+	K^+	K/Na
4831	368.3±30.0	77.3±11.8	0.22±0.04	365.6±33.6	77.2±7.4	0.22±0.03
5971	391.0±52.3	59.7±16.8	0.18±0.06	485.0±83.0	82.2±14.3	0.17±0.02
17729	430.0±47.7	91.2±11.0	0.22±0.03	389.0±31.4	84.6±5.9	0.22±0.02
S. Cappelli	412.0±49.7	63.2±5.1	0.17±0.03	541.2±79.8	79.7±11.7	0.15±0.01
Sham 1	427.2±21.1	59.7±11.2	0.14±0.02	551.5±112.5	83.5±36.5	0.17±0.10

	200 mol m^{-3} NaCl		
Entry	Na^+	K^+	K/Na
4831	499.0±40.7	70.2±10.8	0.14±0.03
5971	568.7±38.3	76.0±13.3	0.14±0.03
17729	545.2±72.9	79.3±15.8	0.12±0.01
S. Cappelli	424.3±11.0	69.2±9.4	0.19±0.02
Sham 1[a]	-	-	-

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[a] not enough green material to make the missing measurements.

Table 61. Mean values (± s.e.) of chloride (Cl^-), nitrate (NO_3^-), orthophosphate (PO_4^{3-}) and sulphate (SO_4^{2-}) ion concentration (mol m^{-3} expressed sap) of five durum wheat entries at five salt external concentrations. Experiment Bangor 1990.

	control				50 mol m^{-3} NaCl			
Entry	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}
4831	35.6±2.2	182.0±8.0	27.7±1.1	3.1±0.6	174.7±14.8	68.6±13.5	51.1±4.5	4.0±0.5
5971	45.2±3.2	124.2±9.3	54.3±2.3	3.8±0.9	217.7±20.6	28.5±11.0	78.2±6.1	0.0±0.0
17729	48.0±3.5	115.0±18.5	64.0±7.1	4.5±1.2	182.3±13.1	52.7±1.8	56.3±3.8	0.0±0.0
S. Cappelli	43.9±3.4	106.0±18.1	56.1±7.3	3.7±0.6	236.2±10.5	41.8±10.0	81.4±6.4	0.6±0.6
Sham 1	40.4±4.0	146.6±11.7	51.4±5.1	2.0±0.5	184.6±4.46	31.6±5.05	75.0±8.01	0.8±0.4

	100 mol m^{-3} NaCl				150 mol m^{-3} NaCl			
Entry	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}
4831	298.0±39.5	20.2±6.5	71.7±11.2	3.3±0.8	357.2±60.0	16.2±6.4	48.0±10.0	1.0±0.6
5971	362.2±103.9	6.5±5.5	110.2±16.6	0.0±0.0	492.5±131.3	5.5±2.6	115.5±22.8	0.0±0.0
17729	305.2±43.8	13.2±5.0	166.5±10.6	0.7±0.7	363.8±37.8	3.0±2.0	114.8±8.5	0.0±0.0
S. Cappelli	378.0±64.9	4.2±2.0	136.5±16.2	0.0±0.0	590.2±109.5	1.0±0.0	62.7±8.8	0.0±0.0
Sham 1	369.8±53.4	5.8±2.2	80.2±14.5	1.7±0.8	712.5±75.5	1.0±0.0	59.0±3.0	0.0±0.0

	200 mol m^{-3} NaCl			
Entry	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}
4831	555.3±99.1	1.0±0.0	55.5±10.3	2.7±1.3
5971	551.7±96.1	1.0±0.0	143.3±49.8	0.3±0.3
17729	538.0±72.8	1.0±0.0	99.2±12.0	0.2±0.2
S. Cappelli	426.3±55.7	1.0±0.0	78.7±15.2	0.0±0.0
Sham 1[a]	-	-	-	-

[a] not enough green material to make the missing measurements.

experiments (reviewed in Munns and Termaat (1986)). Entry '4831' seemed to discriminate between Cl^- and NO_3^- better than the other lines. Indeed, this entry showed the lowest concentration of Cl^- and the highest of NO_3^- among all accessions at each salinity level until 150 mol m^{-3} NaCl. Such discrimination ability should be constitutive in '4831' as it was also present in the control treatment. Competition was also observed for the uptake of the two monovalent cations (Na^+ and K^+) at 50 mol m^{-3} NaCl. Beyond this concentration, the Na^+ content increased on increasing the external NaCl concentration, while the K^+ concentration remained almost constant.

Table 62 summarizes the results of the combined ANOVA performed on all the recorded traits. Salinity levels were always highly different ($P \leq 0.01$), while the entries differed for most characters. Differences among entries were not different for fresh weight:green fresh weight ratio, osmotic potential, K/Na ratio, and Cl^- concentration. The 'entry x salinity level' interaction was significant ($P \leq 0.05$) for all ion concentrations and for the osmotic potential.

Differences among salt treatments for all characters are shown in Table 63. There was a clear decrease in shoot weight until 150 mol m^{-3} external NaCl. At 100 mol m^{-3} NaCl and beyond the stress became significant in terms of leaf necrosis, as indicated by the calculated weight ratio. For the osmotic potential and for both Na^+ and Cl^- concentration the mean values increased progressively from the control treatment to the treatment with 200 mol m^{-3} NaCl. The control treatment had a K^+ content significantly higher than those of all other treatments, which did not differ among themselves. As regards the other anions, the concentration of NO_3^- markedly declined from the control treatment to the highest NaCl content. PO_4^{3-} increased beyond 50 mol m^{-3} NaCl, the highest content being recorded at 100 mol m^{-3} NaCl, while SO_4^{2-} decreased progressively from the control treatment to the treatment with 200 mol m^{-3} NaCl. The concentration of this latter anion was, however, very low in each salt treatment.

Table 62. Results of the analysis of variance performed on various measured parameters on five durum wheat accessions. Experiment Bangor 1990.

Source of variation	df	Mean square	df	Mean square
		Fresh weight		Green fresh weight
entry	4	4.6 ***	4	4.4 ***
salinity level	4	54.8 ***	4	55.5 ***
entry x salinity level	16	0.9 ns	16	0.9 ns
error	136	0.8	136	0.8
		Weights ratio		Osmotic potential
entry	4	0.1 ns	4	44082.9 ns
salinity level	4	1.3 **	4	1729445.9 ***
entry x salinity level	16	0.2 ns	15	95329.5 *
error	127	0.2	78	43449.8
		Na^+		K^+
entry	4	8772.0 *	4	2142.3 **
salinity level	4	960051.0 ***	4	160287.9 ***
entry x salinity level	15	9688.4 **	15	887.7 *
error	85	3401.1	85	425.6

(continued next page)

Table 62 (continued).

Source of variation	df	Mean square	df	Mean square
		K^+/Na^+		Cl^-
entry	4	26.0 ns	4	6761.6 ns
salinity level	4	4086.2 ***	4	902891.8 ***
entry x salinity level	15	19.0 ns	15	23653.1 *
error	85	18.1	87	12046.9
		NO^-		PO_4^{3-}
entry	4	3380.3 ***	4	11007.4 ***
salinity level	4	83611.7 ***	4	13330.5 **
entry x salinity level	15	1299.0 ***	15	2028.2 ***
error	87	279.9	87	578.3
		SO_4^{2-}		
entry	4	18.5 ***		
salinity level	4	35.1 **		
entry x salinity level	15	5.5 **		
error	87	2.2		

ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 63. Salt treatment mean values for various measured parameters on five durum wheat accessions. The ion concentrations are in mol m^{-3} expressed sap. Experiment Bangor 1990.

Salt treatment	Fresh weight (g)	Green fresh wght. (g)	Weights ratio	Osmotic potential (mOsmol kg^{-1})	Na^+	K^+	K^+/Na^+
Control	3.74 a	3.63 a	1.04 c	465.8 c	10.6 d	244.7 a	27.6 a
50 mol m^{-3} NaCl	2.15 b	2.04 b	1.08 c	620.3 c	274.3 c	72.1 b	0.3 b
100 mol m^{-3} NaCl	1.33 c	1.17 c	1.17 bc	850.5 b	405.0 b	69.4 b	0.2 b
150 mol m^{-3} NaCl	0.65 d	0.51 d	1.50 a	1027.5 ab	449.0 ab	81.2 b	0.2 b
200 mol m^{-3} NaCl	0.56 d	0.43 d	1.40 ab	1200.9 a	510.3 a	72.9 b	0.1 b

Salt treatment	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}
Control	42.1 d	136.3 a	49.2 c	3.4 a
50 mol m^{-3} NaCl	198.2 c	44.2 b	68.9 bc	1.3 b
100 mol m^{-3} NaCl	344.0 b	10.0 c	109.1 a	1.3 b
150 mol m^{-3} NaCl	468.0 a	6.2 c	82.2 ab	1.1 b
200 mol m^{-3} NaCl	526.1 a	1.0 c	87.2 ab	0.2 b

Means followed by the same letter in each variable are not different at $P \leq 0.05$ according to Duncan's multiple range test.

The five accessions had rather different patterns of response in terms of aerial biomass to increasing salinity levels. Table 64 shows the entry ratios between mean green fresh weight at the various levels and the mean weight in the control (the results for the shoot fresh weight were fully comparable to these). It is evident that '5971' and, to a lesser extent, 'S. Cappelli' already experienced a drastic effect of salt at 50 mol m^{-3} NaCl. However, as in the experiment Tel Hadya 1989, 'S. Cappelli' and '17729' seemed somewhat less affected than the other entries at 100 mol m^{-3} NaCl. In the case of the former accession, its better "tolerance" at this salinity level was also accompanied by the highest absolute shoot weight (Table 59). The shoot weight of '17729' decreased relatively less than that of the other entries until 200 mol m^{-3} NaCl.

7.1.2 *Experiment Durum-2*

From a screening of low-salt-grown seedlings for ^{22}Na uptake (see below, experiment BAN-1, section 7.2.1), eight accessions with very low ^{22}Na uptake and eight with very high uptake (higher than the tetraploid cultivar 'S. Cappelli') were selected for the present test. 'S. Cappelli' and the hexaploid cultivar 'Probred' were also included as check lines. Five seeds per entry were germinated in rockwool plugs in a P180 plug-tray with one seed per cell and one entry per row of cells. The tray was suspended over a container of aerated "Phostrogen"-based nutrient solution (Gorham *et al.*, 1984) and kept in a greenhouse during February with a minimum temperature of about 15° C and natural daylight supplemented by 400 W Son-T sodium vapour lamps to give a photoperiod of 16 hrs. After three days salt was added to the nutrient solution to a level of 50 mol m^{-3} NaCl which was maintained throughout the experiment. The youngest, fully-expanded leaf was harvested after

Table 64. Mean shoot green fresh weight of five durum wheat entries at increasing NaCl external concentration, relative to the mean weight in the control treatment. Experiment Bangor 1990.

Entry	50:control[a]	100:control	150:control	200:control
4831	0.60	0.25	0.11	0.11
5971	0.37	0.23	0.18	0.13
17729	0.67	0.43	0.27	0.19
S. Cappelli	0.54	0.45	0.13	0.14
Sham 1	0.74	0.35	0.11	0.05
Mean	0.58	0.34	0.16	0.12
s.e.	0.06	0.04	0.03	0.02

[a] 50 = 50 mol m^{-3} NaCl; 100 = 100 mol m^{-3} NaCl; 150 = 150 mol m^{-3} NaCl; 200 = 200 mol m^{-3} NaCl.

two weeks at this salinity from five plants of each entry. The samples were placed in microcentrifuge tubes and frozen. Sap was extracted from frozen/thawed and crushed samples by centrifugation at 5000 g for five minutes. The centrifuged extract was diluted (20 μl sap : 5 ml H_2O = 1 : 250) and used for the determination of Na and K concentration in a flame photometer.

Differences between entry means for Na and K content and for the K/Na ratio were tested by an analysis of variance (ANOVA). The mean values of the durum wheat entries were compared among themselves by the Newman and Keuls test, and with the mean values of the hexaploid check cultivar 'Probred' by Dunnett's test.

Table 65 shows the results for cation concentration measurements made on leaves of the 16 selected durum wheat entries, of 'S. Cappelli' and of 'Probred' grown at 50 mol m^{-3} NaCl external concentration. Highly significant differences were observed among the tetraploid entries for both Na and K concentration as well as for the cation ratio. As expected, there was a significant difference between the hexaploid check cultivar and the tetraploid accessions for K/Na ratio, while most entries differed significantly ($P \leq 0.05$) from 'Probred' in terms of Na and K concentration. Entry '38584' showed an interesting low Na content, while '19606' had a high K concentration accompanied by a relatively low Na concentration. As a result of these characteristics, the two above-mentioned accessions had the highest K/Na ratio among all tetraploid entries. For this reason they were included in a sand-culture evaluation carried out in Syria (experiment Tel Hadya 1990, section 6.2.2). In that experiment, both accessions ranked best out of seven entries for shoot weight across salinity levels and '19606', in particular, presented a very interesting pattern of response to the stress.

Table 65. F-test results for Na^+ and K^+ leaf concentration ($mol\ m^{-3}$ expressed sap) and K/Na ratio measured on 17 durum wheat entries and the hexaploid cultivar 'Probred', and comparison among tetraploid entry means and between tetraploid entry means and 'Probred' means. Salt external concentration: 50 $mol\ m^{-3}$ NaCl. Experiment Durum-2.

Entry	% of 'S. Cappelli' uptake in experiment BAN-1		Na	K	K/Na ratio
		F-test[a]:	***	**	***
4097	4		99.6 ♦ ab	110.6 ♦ b	1.23 ♦ b
3449	6		61.4 ♦ abcd	105.0 ♦ b	2.00 ♦ b
3157	7		71.2 ♦ abcd	101.6 ♦ b	1.55 ♦ b
7599	9		100.0 ♦ ab	88.2 ♦ b	0.89 ♦ b
3249	10		39.2 cd	83.4 ♦ b	2.16 ♦ b
5420	12		56.4 ♦ bcd	105.4 ♦ b	1.91 ♦ b
18038	16		66.0 ♦ abcd	108.8 ♦ b	1.81 ♦ b
M21	20		106.6 ♦ a	105.2 ♦ b	0.99 ♦ b
S. Cappelli	-		84.6 ♦ abc	121.0 ♦ ab	1.48 ♦ b
10115	104		53.2 ♦ bcd	102.4 ♦ b	1.93 ♦ b
18281	110		75.6 ♦ abcd	129.6 ab	1.81 ♦ b
13606	114		87.0 ♦ ab	126.4 ab	1.52 ♦ b
20418	124		96.6 ♦ ab	103.4 ♦ b	1.10 ♦ b
7660	125		75.2 ♦ abcd	125.2 ab	1.71 ♦ b
20078	126		88.2 ♦ ab	102.6 ♦ b	1.46 ♦ b
38584	130		30.6 d	108.6 ♦ b	3.61 ♦ a
19606	139		53.4 ♦ bcd	159.2 a	3.46 ♦ a
Probred (6X)	0.05		1.2	167.2	149.40

[a] ** and *** : significant at $P \leq 0.01$ and $P \leq 0.001$, respectively.

Entry means in each column followed by ♦ are different ($P \leq 0.05$) from 'Probred' according to Dunnett's test.

Entry means in each column followed by the same letter are not different ($P \leq 0.05$) from each other according to Newman and Keuls test.

7.2 *Laboratory experiments*

The accumulation of ^{22}Na in the shoots of low-salt-grown seedlings has been used as a test of the presence of the enhanced K/Na discrimination character. Measurements of ^{22}Na fluxes into intact seedlings exposed to low concentrations of salt are feasible. They have been made, essentially as described by Jeschke and Jambor (1981), on diploid, tetraploid and hexaploid wheats, as well as on other *Triticeae* (Gorham *et al.*, 1990a; Gorham *et al.*, 1990b; Gorham and Wyn Jones, 1990b; Gorham *et al.*, 1991; Nevo *et al.*, 1992). At the species level there is a good correlation between enhanced K/Na discrimination and ^{22}Na accumulation in low-salt seedlings. Within species there appears to be more variation for ^{22}Na uptake than for leaf Na concentrations. The relationship between ^{22}Na and leaf Na seems less evident within species than between species (Gorham, 1993).

A series of tests were carried out on durum wheat entries from the ICARDA collection in the assumption that any difference in sodium accumulation at high salinity, indicating possibly different K/Na discrimination, could be related to different ^{22}Na uptake at low salt concentration.

7.2.1 *Measurements of ^{22}Na fluxes into low-salt-grown seedlings. Experiment BAN-1*

Seventy entries were used, representing a wide sample of germplasm varying for origin (18 countries being represented) and agronomic characteristics. The procedures described in Gorham *et al.* (1990b) were followed. Seeds were imbibed overnight in slowly flowing tap water, and germinated at 25° C on moist capillary matting attached beneath a plug tray suspended over aerated 0.5 mol m^{-3} $CaSO_4$ solution (pH 5.5). The seedlings were grown in a FISONS 600 THTL growth cabinet maintained at 22° C with a 16 hrs. photoperiod. After two days seedlings were grown for a further four days over 2 mol m^{-3} $Ca(NO_3)_2$ + 1 mol m^{-3} $MgSO_4$ (pH 5.4). The seedlings were incubated for 48 hrs. in a solution of 1 mol m^{-3} NaCl + 0.1 mol m^{-3} KCl containing 148 kBq of ^{22}Na. At the end of the incubation the shoots were excised and weighed. ^{22}Na in shoot tissue was measured in a well-type gamma counter with a 76 mm diameter NaI crystal contained within a 49 mm thick lead shield.

The 70 entries were split into six sets, one of which included also the tetraploid variety 'Langdon' and the hexaploid variety 'Probred'. The durum wheat variety 'S. Cappelli' was used in each batch of entries as a check line to account for variation in incubation conditions. Each set included a tray with 13 entries, one entry per row of 10 cells and two seeds per cell. 'S. Cappelli' was always placed in the seventh row of cells. Ten measurements per entry were made. The results of any set were expressed relative to the uptake into the control 'S. Cappelli' in that set. This enabled comparison of the results originating from different sets.

Table 66 shows the entry frequency in different ^{22}Na uptake classes (relative to 'S. Cappelli'). The wheat varieties 'Probred' and 'Langdon' had an uptake of 5% and 118% relative to 'S. Cappelli', respectively. These results are in agreement with previous observations (Gorham, 1993) on the differences of ^{22}Na uptake between durum and bread wheat, which reflect the absence of the enhanced K/Na discrimination character in the cultivated tetraploid wheats (Gorham *et al.*, 1991). However, the ^{22}Na uptake varied widely among the ICARDA accessions, with values ranging from 4% to 139% of 'S. Cappelli' uptake. The lowest ranking entries had results comparable to those of the hexaploid check 'Probred'. It was interesting to note that the seven entries with the lowest uptake were all

Table 66. Entry frequency in different ^{22}Na uptake classes of 70 durum wheat entries. Experiment BAN-1.

Class intervals (% of 'S. Cappelli' uptake)	Frequency
< 10	12
11 - 20	12
21 - 30	4
31 - 40	3
41 - 50	5
51 - 60	4
61 - 70	5
71 - 80	6
81 - 90	4
91 - 100	2
101 - 110	4
111 - 120	2
121 - 130	5
> 130	2

landraces from Ethiopia ('3402', '4097', '3267', '3449', '3892', '3157' and '3540'). In order to make sure that the entries with low ^{22}Na uptake were tetraploid wheat accessions, the somatic chromosome number was determined on 15 entries the uptake of which ranged between 4% and 33% of 'S. Cappelli' uptake. Two roots, about 10 mm long, were excised from each seedling, treated with a saturated aqueous solution of 1-bromonaphthalene for 4.5 hrs., fixed with glacial acetic acid and Feulgen stained. Five to ten seedlings per accession were examined. All the checked entries were confirmed as tetraploid.

The set of 70 entries tested also included 33 entries used together with 'S. Cappelli' in the experiment Tel Hadya 1989 (section 6.2.1). These had an uptake ranging between 4% and 133% of 'S. Cappelli'. The four entries '4831', '5971', '17729' and 'Sham 1' had a ^{22}Na uptake equal to 26%, 83%, 63% and 29% of 'S. Cappelli' uptake. The two entries added to the experiment Tel Hadya 1990 ('19606' and '38584') had, respectively, an uptake of 139% and 130% relative to 'S. Cappelli'. These values were among the highest recorded in the present experiment.

In an attempt to highlight possible relationships between morphological characters and ^{22}Na uptake, simple correlation coefficients were computed between measured ^{22}Na in the experiment BAN-1 and all the characters recorded in the control treatment of the experiment Tel Hadya 1989 for the 34 accessions common to the two trials. ^{22}Na uptake (relative to 'S. Cappelli') was significantly correlated only with the lamina area both of the youngest, fully expanded leaf in the early harvest and of the flag-leaf in the final harvest at Tel Hadya 1989, though the correlation coefficients were not outstanding ($r=0.42$, $P<0.05$, in the former case; $r=0.36$, $P<0.05$, in the latter). It would seem that the accessions with larger leaves tended to accumulate more ^{22}Na per unit of shoot fresh weight (the measurements of ^{22}Na were all expressed in Bq mg^{-1} of shoot fresh weight and then related to the uptake of 'S. Cappelli'). The Ethiopian landraces generally had rather small leaves and accumulated little ^{22}Na. The Ethiopian germplasm appeared in other experiments as distinct from any other gene pool for several morphological and physiological traits (Harlan, 1969; Qualset and Puri, 1975; Pecetti *et al.*, 1992a; Pecetti *et al.*, 1992c).

7.2.2 *Measurements of ^{22}Na fluxes into seedlings grown at different NaCl external concentrations. Experiment BAN-2*

From the above experiment six accessions with higher uptake and six with lower uptake than 'S. Cappelli' were chosen, together with 'S. Cappelli', for a further screening with the same sodium isotope. The methodology was the same as that described in the previous section, with the difference that two treatments were used, namely 1 mol m^{-3} NaCl + 1 mol m^{-3} KNO$_3$, and 25 mol m^{-3} NaCl + 1 mol m^{-3} KNO$_3$. Five measurements per entry were made at each salt concentration.

Table 67 reports the results of this further study on ^{22}Na uptake. It is evident that in the screening at a Na$^+$: K$^+$ = 1 concentration, the two groups of high- and low-uptake entries remained somewhat distinct, with a mean uptake of 74.5 Bq mg^{-1} shoot fresh weight and 43.2 Bq mg^{-1} shoot fresh weight, respectively (different at $P \leq 0.05$ according to t-test). However, the difference was much reduced in comparison with the first screening carried out in BAN-1, when the same NaCl external concentration was used (1 mol m^{-3}) but with a Na$^+$: K$^+$ = 10 ratio. By contrast, at a Na$^+$: K$^+$ = 25 concentration the difference between the two groups of entries was not significant, the mean uptake values being 237.0 Bq mg^{-1} shoot fresh weight and 229.8 Bq mg^{-1} shoot fresh weight for high- and low-uptake entries, respectively.

Table 67. Mean ^{22}Na uptake (Bq mg^{-1} shoot fresh weight) and uptake value relative to 'S. Cappelli' of 12 durum wheat entries incubated at two different salt external concentrations. Experiment BAN-2.

		Salt external concentration			
		1 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3		25 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3	
Entry	% of 'S. Cappelli' uptake in experiment BAN-1	Mean ± s.e.	% of S. Cappelli	Mean ± s.e.	% of S. Cappelli
3402	4	45 ± 2	71	190 ± 19	81
3157	7	53 ± 4	84	195 ± 19	84
3540	9	45 ± 5	71	236 ± 50	101
3772	10	43 ± 7	69	165 ± 15	71
3249	10	45 ± 9	71	342 ± 157	147
7599	9	28 ± 8	44	294 ± 66	126
S. Cappelli	-	63 ± 7	-	233 ± 72	-
19606	139	75 ± 8	118	193 ± 13	83
16566	133	97 ± 4	152	247 ± 64	106
38584	130	62 ± 7	98	181 ± 21	78
20078	126	73 ± 15	116	126 ± 6	54
7660	125	82 ± 9	130	398 ± 106	170
20418	124	58 ± 1	91	234 ± 43	100

7.2.3 Measurements of ^{22}Na and ^{86}Rb fluxes into durum wheat seedlings. Experiment BAN-3

The 13 entries used in the experiment BAN-2 (section 7.2.2) were also included in a further test which investigated the uptake of both Na^+ and K^+. The ^{22}Na radioisotope was used as the tracer for Na^+, while ^{86}Rb was used as the tracer for potassium. The adoption of ^{86}Rb to label K^+ in flux studies has been reported in different cereal species such as maize (Leigh and Wyn Jones, 1975), oats (Mills *et al.*, 1985), barley (Behl and Jescke, 1982; Lynch and Läuchli, 1984; Siddiqi and Glass, 1987) and rice (Aramrattana and Scott, 1987). The experimental protocol was as described in section 7.2.1, with the difference that two vessels were used with the same external salt concentration (50 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3). In one container the seedlings were incubated in solution containing 148 kBq of ^{22}Na, while in the other 1480 kBq of ^{86}Rb were added to the salt solution. Ten measurements per entry were made for both ^{22}Na and ^{86}Rb, using the same gamma counter described in section 7.2.1.

The results of this experiment are shown in Table 68. The two groups of low- and high-uptake of ^{22}Na in BAN-1 did not significantly differ for ^{22}Na content at 50 mol m^{-3} NaCl (the mean values were, respectively, 439.3 Bq mg^{-1} shoot fresh weight and 390.7 Bq mg^{-1} shoot fresh weight), suggesting once again that the discrimination among accessions for this character is possible only in low-salt-grown seedlings. The two groups did differ significantly ($P \leq 0.01$, according to t-test) for ^{86}Rb uptake. The low-^{22}Na-uptake entries in BAN-1 had a lower mean uptake of ^{86}Rb (340.8 Bq mg^{-1} shoot fresh weight) than the high-^{22}Na-uptake entries (487.8 Bq mg^{-1} shoot fresh weight).

Table 68. Mean ^{22}Na and ^{86}Rb uptake (Bq mg^{-1} shoot fresh weight) and uptake values relative to 'S. Cappelli' of 12 durum wheat entries incubated at 50 mol m^{-3} NaCl + 1 mol m^{-3} KNO$_3$ external concentration. Experiment BAN-3.

Entry	% of 'S. Cappelli' uptake in experiment BAN-1	^{22}Na uptake Mean ± s.e.	^{22}Na uptake % of S. Cappelli	^{86}Rb uptake Mean ± s.e.	^{86}Rb uptake % of S. Cappelli
3402	4	675 ± 67	181	249 ± 25	54
3157	7	422 ± 54	113	297 ± 46	64
3540	9	359 ± 21	97	416 ± 79	90
3772	10	394 ± 15	106	429 ± 34	93
3249	10	414 ± 9	111	290 ± 26	63
7599	9	392 ± 17	105	364 ± 27	79
S. Cappelli	-	372 ± 20	-	462 ± 39	-
19606	139	386 ± 20	104	488 ± 43	106
16566	133	413 ± 43	111	545 ± 81	118
38584	130	342 ± 13	92	554 ± 31	120
20078	126	426 ± 25	114	428 ± 30	93
7660	125	397 ± 22	107	445 ± 24	96
20418	124	380 ± 13	102	467 ± 47	101

7.2.4 *Measurements of ^{22}Na uptake into low-salt-grown seedlings. Experiment BAN-4*

The seven durum wheat entries evaluated in the experiment Tel Hadya 1990 (section 6.2.2.), viz., '4831', '5971', '17729', 'Sham 1', 'S. Cappelli', '19606' and '38584', underwent a screening for ^{22}Na uptake at low NaCl external concentration during March 1993. The bread wheat cultivar 'Probred' was included for comparison. The same methodology as the previously described radioisotope measurements was adopted. Five-day-old low-salt seedlings of the eight entries were incubated in a solution of 1 mol m^{-3} NaCl and 1 mol m^{-3} KNO_3 containing 148 kBq of ^{22}Na. Ten measurements per entry were made.

The results of this experiment are summarised in Table 69. Entry mean values differed significantly ($P \leq 0.001$). As expected on the basis of previous experimental evidence (section 7.2.1) the hexaploid variety 'Probred' had the lowest ^{22}Na uptake. 'Sham 1' and '4831' presented values of ^{22}Na concentration higher than 'Probred' but, at the same time, lower than those of all other tetraploid accessions.

7.2.5 *Relationships among cation measurements in different experiments*

In order to assess possible relationships among the cation concentrations recorded in different experiments carried out at Bangor, a correlation matrix was calculated using data from accessions which were common to any pair of experiments (Table

Table 69. Mean ^{22}Na uptake (Bq mg^{-1} shoot fresh weight) of seven durum wheat entries and the hexaploid cultivar 'Probred' incubated at 1 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3 external concentration. Experiment BAN-4.

Entry	Mean ± s.e.	
17729	7.5 ± 0.9	a
5971	7.0 ± 0.7	ab
38584	7.0 ± 0.3	ab
19606	6.6 ± 0.4	ab
S. Cappelli	5.7 ± 0.3	b
Sham 1	4.1 ± 0.3	c
4831	3.9 ± 0.2	c
Probred (6X)	1.5 ± 0.2	d

Means followed by the same letter are not different at $P \leq 0.05$ according to the Newman and Keuls test.

70). The characters entered in the matrix were the following: ^{22}Na uptake at 1 mol m^{-3} NaCl external concentration relative to 'S. Cappelli', recorded in the experiment BAN-1 (coded as "^{22}Na BAN-1" in the matrix); ^{22}Na uptake at 1 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3 external concentration, recorded in the experiment BAN-2 (coded as "^{22}Na BAN-$2_{(1:1)}$"); ^{22}Na uptake at 25 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3 external concentration, recorded in the experiment BAN-2 (coded as "^{22}Na BAN-$2_{(25:1)}$"); ^{22}Na and ^{86}Rb uptake at 50 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3 external concentration, recorded in the experiment BAN-3 (coded as "^{22}Na BAN-3" and "^{86}Rb BAN-3", respectively); ^{22}Na uptake at 1 mol m^{-3} NaCl + 1 mol m^{-3} KNO_3, recorded in the experiment BAN-4 (coded as "^{22}Na BAN-4"); Na and K concentration (mol m^{-3} expressed sap) in youngest, fully-expanded leaves of plants grown at 50 mol m^{-3} NaCl external concentration, recorded in the experiment Durum-2 (coded as "Na Dur-2" and "K Dur-2", respectively). Given the limited number of observations in common between any pair of experiments, a probability level $P \leq 0.10$ was retained as sufficient instead of the usual $P \leq 0.05$ to reject the null hypothesis of $r = 0$.

In spite of this limited number of observations, some trends were evident. There was a positive correlation between the ^{22}Na uptake in the experiments with the lower NaCl external concentration (1 mol m^{-3}, either with or without a Na : K ratio = 1) and both K and ^{86}Rb adsorption at 50 mol m^{-3} NaCl external concentration. A positive correlation existed between ^{22}Na uptake in the three experiments with 1 mol m^{-3} NaCl concentration. ^{86}Rb uptake at 50 mol m^{-3} NaCl was positively correlated with K concentration measured at 50 mol m^{-3} NaCl, and negatively correlated with ^{22}Na uptake at the same NaCl external concentration. There was no correlation between ^{22}Na adsorption in low-salt-grown seedlings and both ^{22}Na and Na uptake at higher salinity levels (25 and 50 mol m^{-3} NaCl). Quite surprisingly, there was no correlation between Na and K concentration values measured on 17 durum wheat entries grown at 50 mol m^{-3} NaCl (experiment Durum-2).

8 *Comparison of screening methods for salinity resistance*

8.1 *Overall comparison (experiments Tel Hadya 1989, Tel Hadya 1990 and Bangor 1990)*

Three of the previously described experiments (Tel Hadya 1989, Tel Hadya 1990 and Bangor 1990) included a common set of entries ('4831', '5971', '17729', 'Sham 1' and 'S. Cappelli'), two common salt treatments (the control and 100 mol m^{-3} NaCl), and the common assessment of biological yield (expressed as shoot fresh weight) after four weeks of growth at the desired salt content. These common factors enabled assessment of the relative effect of different salinity levels, of different growth seasons, or of different growth media on the entry responses. In other words, it was possible to assess the consistency and reliability of results originating from the same set of materials grown under different environmental conditions. For that reason, an analysis of variance was performed according to the suggestions of Cochran and Cox (1957, chapter 14) on the analysis of a series of experiments. In particular, as the present analysis presented heterogeneity of experimental error variances (Hartley's test of equality of experimental error variances rejected at $P \leq 0.05$), the pooled error mean square for insertion in the analysis was calculated as described by Cochran and Cox (1957, p. 558) for the analysis of such a case. 'Experiment' and 'salinity level' were considered fixed factors while 'entry' was considered random. The latter factor was considered random in order to make the comparison between experiments and treatments as general as possible and not too related to the specific set of materials used in this assessment. 'Experiment' mean square was tested on 'entry x experiment' mean square. Similarly, 'salinity level' mean square was tested on 'entry x salinity level' mean square. 'Salinity level x experiment' mean square was tested on the 'entry x salinity level x experiment' interaction mean square. The sum of squares and degrees of freedom of the factor 'experiment' and of the interaction 'entry x experiment' were partitioned to give an orthogonal set of comparisons (Steel and Torrie, 1960, chapter 11). The comparisons of interest were between the means of: i) the experiment in Bangor and the average of the two experiments in Tel Hadya; and ii) the two experiments in Tel Hadya. The analysis also assessed the entry interaction with different experiments: Bangor versus Tel Hadya (average of the two experiments), and Tel Hadya 1989 versus Tel Hadya 1990. The mean square of each contrast between experiments was tested on the respective interaction with 'entry'. All remaining mean squares were tested on the pooled error mean square.

At each salinity level in each experiment entry mean values for the character shoot fresh weight (FW) were compared by Duncan's multiple range test.

In Table 71 the mean squares and respective F-values originating from the described ANOVA for the character shoot fresh weight are reported. The three experiments, on the whole, differed at 5% probability. The contrast comparing Bangor and the average of Tel Hadya experiments was not significant, while the contrast between Tel Hadya 1989 and Tel Hadya 1990 was significant at 1% probability. The different conditions experienced by the materials in the Syrian location during the two growing periods (autumn-winter in 1989 and spring-summer in 1990) must have resulted in large differences in terms of plant growth. As expected, salinity levels (the control and 100 mol m^{-3} NaCl) differed significantly. The interaction between experiments and salinity levels was significant at 5% probability. Differences among entries were highly significant. This result confirmed the variability among the five accessions, on the basis of which they were chosen. The entries strongly interacted with the three experiments. Moreover,

Table 71. Results of the analysis of variance combining the factors 'experiment', 'salinity level' and 'entry' performed on the character shoot fresh weight recorded in the experiments Tel Hadya 1989 (early harvest), Tel Hadya 1990 and Bangor 1990.

Source of variation	df	MS	F[a]
Experiment	2	170.7	7.49 *
- Bangor vs. Tel Hadya	1	55.9	2.07 ns
- Tel Hadya 1989 vs. Tel Hadya 1990	1	327.5	11.21 *
Salinity level	1	79.0	35.14 **
Entry	4	50.0	118.73 ***
Salinity level x experiment	2	13.0	7.46 *
Entry x experiment	8	22.8	54.13 ***
- Entry x (Bangor vs. Tel Hadya)	4	27.0	64.13 ***
- Entry x (Tel Hadya 1989 vs. Tel Hadya 1990)	4	29.2	69.36 ***
Entry x salinity level	4	2.2	5.34 ***
Entry x salinity level x experiment	8	1.7	4.13 ***
Pooled error	202	0.4	

[a] ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Bangor differed from Tel Hadya in its interaction with entries. The response of entries was also highly different in the two experiments carried out in Tel Hadya. It is evident that this response was largely experiment-specific, even when the experiments were carried out in the same location and with the same methodology. Rawson *et al.* (1988) found a very different genotypic response for NaCl tolerance in two experiments (including barley, bread wheat and durum wheat) carried out with the same cultural conditions but under different external conditions in terms of vernalisation, photoperiod, radiation and thermoperiod.

Highly significant interaction between salinity levels and entries was revealed across experiments (Table 71). A significant, though rather weak, 'entry x salinity level' interaction had already been found in individual experiments (Tel Hadya 1989, Table 45, and Tel Hadya 1990, Table 52). Entries also interacted with the salt content in different manners in the various experiments, as indicated by the highly significant interaction 'entry x salinity level x experiment' (Table 71). That was, for instance, the case of entry '4831', which showed no effect of 100 mol m^{-3} NaCl on shoot fresh weight in Tel Hadya 1989 (Table 44), had a little reduction in Tel Hadya 1990 (Table 51), and had a drastic decrease of fresh weight in Bangor 1990 (Table 64). Previously reported results on different crops (reviewed by Richards (1983b)) always showed 'genotype x salt concentration' interaction.

Table 72 reports the Duncan's test among entry means for shoot fresh weight at each salinity level in each experiment. Mean values in the experiment Tel Hadya 1989 were very different from those in Tel Hadya 1990. However, the ranks at the two salinity levels were rather similar both within each experiment and across the two experiments. The sand-culture screening did not seem to greatly affect the relative response of the materials at different salt contents, even though the absolute values varied as a function of the experiment. Differences in external conditions (temperature, daylength, etc.) probably accounted for the

Table 72. Entry means of the character shoot fresh weight (g) at the two common salinity levels (control and 100 mol m^{-3} NaCl) in three experiments.

	Tel Hadya 1989		Tel Hadya 1990		Bangor 1990	
Entry	control	100 mol m^{-3} NaCl	control	100 mol m^{-3} NaCl	control	100 mol m^{-3} NaCl
4831	1.48 b	1.52 c	1.72 b	1.21 bc	4.90 a	1.33 a
5971	7.53 a	6.15 ab	2.98 ab	1.77 ab	3.98 ab	1.07 a
17729	6.76 a	6.37 ab	3.01 ab	1.74 ab	2.91 ab	1.32 a
S. Cappelli	8.34 a	6.85 a	3.38 a	2.34 a	3.70 ab	1.83 a
Sham 1	2.95 b	3.51 bc	1.61 b	0.90 c	2.57 b	1.01 a

Means followed by the same letter at each salinity level in each experiment are not different at $P \leq 0.05$ according to Duncan's test.

different plant growth observed in the two sand-culture experiments. In contrast, the experiment Bangor 1990 showed a rather different entry ranking. In this experiment there was a kind of "flattening" of the plant response at 100 mol m^{-3} NaCl which caused no difference to be evident among entries. Entry '4831', which was characterised in the sand-culture experiments by one of the lowest growth potentials (measured as the shoot weight in the control treatment), had an opposite behaviour in the hydroponic-culture, showing the highest shoot weight in the control.

8.2 *Comparison between sand-culture and hydroponic-culture for salt resistance assessment. Experiment Bangor 1993*

This experiment aimed at comparing under the same environmental conditions two growing techniques which may be used to screen plant material against salinity stress, i.e., the hydroponic-culture and the sand-culture. The seven durum wheat entries already evaluated in the experiment Tel Hadya 1990 were grown in both media. The experiment was carried out in a greenhouse at Bangor during February-March. Temperature and photoperiod were regulated as described in section 7.1.1. Seeds of the seven entries were germinated in plug-trays filled with a 1:1 (v:v) mixture of compost and vermiculite, placed in a growth cabinet maintained at 22° C. After eight days the seedlings were moved to the greenhouse. The hydroponic-culture was carried out in aerated "Phostrogen"-based nutrient solution contained in plastic tubs of 25 dm^3 volume (Gorham *et al.*, 1984). Two tubs were used, one for the control treatment and one for the treatment with 100 mol m^{-3} NaCl. In each tub, a plug-tray containing the seedlings of the seven entries was suspended over the nutrient solution. The sand-culture was carried out in plastic pots of about 2.5 dm^3 volume: at the bottom a layer of gravel was placed to facilitate the drainage and the rest was filled with coarse sand. For the irrigation of the pots, the same nutrient solution of the hydroponics was used. Each pot received 300 ml of solution every day. Free drainage of the pots was ensured by holes in the bottom. In both growing media each entry was present in each salt treatment with six replications represented by as many seedlings. In the hydroponic-culture the seedlings were placed in each tub according to a completely randomised design. In the sand-culture the six seedlings of each entry were grown in two pots (three in each pot). There was a total of 14 pots (2 pots x 7 entries) in each treatment, which were randomly placed on a greenhouse bench. The six seedlings of each entry were considered as completely randomised in each treatment and the data were analysed accordingly. The two salt treatments of each growing conditions were placed side-by-side on the same bench. The benches for the hydroponics and the sand-culture faced each other at a distance of less than 1 m.

After five days of growth in the greenhouse, salt (NaCl) was added to the tub and to the 14 pots allocated to the stress treatment, at about 33.3 mol m^{-3} day^{-1} for three consecutive days to reach the desired level of 100 mol m^{-3}. $CaCl_2$ was also added in the salt treatment to maintain a nominal Na:Ca ratio of 20:1 (see section 6.2.1.1). The salt was added directly to the aerated nutrient solution in the hydroponic-culture, and to half of the stock nutrient solution used for irrigation in the sand-culture. The solutions both with and without NaCl in both growing conditions were replaced after one week.

After two weeks at full salinity the root and shoot weight of each plant was measured. Care was taken to remove and wash from the sand all the roots grown in the pots. The youngest, fully-expanded and healthy leaf of each plant was placed in a microcentrifuge tube and frozen. Sap was extracted from thawed, crushed leaves by centrifugation, as already described in section 7.1.1. Inorganic ion analysis was then carried out by Dionex 2010i ion chromatograph which measured the concentration of the cations sodium and potassium and of the anions chloride, nitrate, orthophosphate and sulphate. The ratio between potassium and sodium concentration was computed.

At each salinity level in each growing medium entry mean values for all characters were compared by Duncan's multiple range test. Simple correlation coefficients were computed among all recorded characters. The two evaluations in different growing media were considered independent experiments and, therefore, an analysis of variance was performed according to the suggestions indicated by Cochran and Cox (1957, chapter 14) on the analysis of the results of a series of experiments. Unlike the analysis reported in section 8.1, in this case the two experiments had similar experimental error variances (Hartley's test of equality of experimental error variances not rejected at $P \leq 0.05$) for all recorded characters, except K^+ concentration and K/Na ratio. In all cases in which Hartley's test was not rejected the pooled error mean square for insertion in the analysis was computed as the average of the individual experimental error mean squares (Cochran and Cox, 1957, p. 548). For K^+ concentration and K/Na ratio the pooled error mean square was calculated according to the formula indicated by Cochran and Cox (1957, p. 558) for the case of heterogeneity of experimental error variances.

'Entry' was considered a random factor (as in section 8.1), while 'technique' and 'salinity level' were considered fixed. 'Technique' mean square was tested on 'entry x technique' mean square. Similarly, 'salinity level' mean square was tested on 'entry x salinity level' mean square. 'Salinity level x experiment' mean square was tested on 'entry x salinity level x experiment' mean square. All remaining mean squares were tested on the pooled error mean square.

Table 73 reports the Duncan's test among entry means for shoot and root fresh weight at each salinity level in the two growing media. The F-test of the ANOVA was always significant at $P \leq 0.01$ for shoot weight and at $P \leq 0.05$ for

Table 73. Entry mean values (± s.e.) and mean separation of the characters shoot fresh weight (g) and root fresh weight (g) recorded on seven durum wheat entries at two salinity levels (control and 100 mol m^{-3} NaCl) in two growing media (hydroponic-culture and sand-culture). Experiment Bangor 1993.

	Shoots		Roots	
Entry	control	100 mol m^{-3} NaCl	control	100 mol m^{-3} NaCl
	Hydroponic-culture			
S. Cappelli	4.08±0.44 ab	1 3.93±0.40 a	2.85±0.30 b	3.95±0.39 a
Sham 1	3.26±0.29 bc	7 2.43±0.13 c	3.04±0.35 ab	4 2.95±0.31 bc
19606	3.03±0.18 bc	2 3.48±0.28 ab	2.40±0.21 b	2 3.85±0.34 a
4831	4.14±0.28 ab	6 2.55±0.24 bc	2.92±0.25 b	2.23±0.13 c
17729	2.58±0.38 c	5 2.57±0.22 bc	2.24±0.17 b	5 2.77±0.52 bc
38584	4.67±0.30 a	2.97±0.17 bc	3.92±0.29 a	3 3.43±0.49 bc
5971	2.98±0.38 bc	4 2.82±0.41 bc	2.10±0.46 b	5 2.77±0.35 bc
	Sand-culture			
S. Cappelli	5.90±0.61 a	1 3.43±0.24 a	4.28±0.40 a	2.72±0.32 a
Sham 1	3.33±0.30 c	7 1.68±0.15 c	2.85±0.34 bc	5 1.75±0.24 a
19606	5.34±0.34 ab	3.60±0.09 a	3.78±0.37 ab	2 2.70±0.07 a
4831	3.68±0.24 c	6 2.02±0.34 bc	2.07±0.16 c	1.48±0.17 b
17729	4.22±0.38 bc	5 2.10±0.17 bc	3.30±0.25 ab	6 1.68±0.15 b
38584	5.03±0.41 ab	4 2.45±0.25 b	4.12±0.55 a	4 2.15±0.30 ab
5971	4.38±0.46 bc	3 2.48±0.13 b	3.73±0.47 ab	3 2.58±0.38 a

In each group of means, values followed by the same letter are not different at $P \leq 0.05$, according to Duncan's test.

root weight in the hydroponic-culture (at both salt contents). The same test was significant at $P \leq 0.001$ for shoot weight and at $P \leq 0.01$ for root weight in the sand-culture. The latter screening techniques had, therefore, a better ability to discriminate the materials under evaluation as far as the plant weight was concerned.

It appears that the root growth in the control treatment of the hydroponics was somewhat odd, the entry mean values in this treatment being in several cases lower than those in the stress treatment (although the overall means of the two treatments were not significantly different, as shown later in Table 77), unless a positive effect of NaCl on root growth in the hydroponic-culture has to be postulated. To some extent, the stuntedness in the control treatment (or the paradoxically better growth in the stress treatment) appeared also for the shoots. Indeed, only 'Sham 1', '4831' and '38584' had an appreciable reduction of shoot weight due to the stress, relative to the control.

'Sham 1' and '4831' confirmed their relatively poor growth potential under sand-culture conditions, as already seen in the experiments Tel Hadya 1989 and Tel Hadya 1990. Entry '19606', which proved the most interesting in the experiment Tel Hadya 1990, is again worth mentioning. This Syrian landrace had some of the highest shoot and root weights at 100 mol m^{-3} NaCl in both hydroponics and sand-culture, in both absolute terms and as percent of controls. The behaviour of '19606' suggests for this entry some "physiological" tolerance, defined as a small reduction in growth due to salinity (Rawson *et al.*, 1988), and "absolute" tolerance, shown as an intrinsic high growth rate (Rawson *et al.*, 1988). Though slightly more affected by the stress treatment, 'S. Cappelli' was another interesting accession, with similar characteristics to those of '19606'.

The concentrations of the monovalent cations Na^+ and K^+ at 100 mol m^{-3} NaCl for each entry are shown in Table 74. The F-test of entry mean values was highly significant ($P \leq 0.01$) in both screening methods for the K^+ concentration and for the K/Na ratio. The F-test for Na^+ content was significant at $P \leq 0.001$ in the hydroponics, and at $P \leq 0.10$ in the sand-culture which seemed, therefore, less capable to discriminate among entries for sodium uptake under stress.

It is evident that in the hydroponic-culture '4831', 'Sham 1' and '19606' absorbed relatively less Na^+ and relatively more K^+ than the other entries, and their K/Na mean ratios were the highest (Table 74). In particular, 'Sham 1' had the least increase of Na^+ at 100 mol m^{-3} NaCl relative to the control (36.9-fold), while '19606' had the least decrease of K^+ (0.54-fold). This latter entry had been noted in the experiment Durum-2 (section 7.1.2) for its high K^+ and rather low Na^+ concentration (relatively to other tetraploid entries) at 50 mol m^{-3} NaCl, which resulted in a K/Na ratio > 2.5 (see Table 65). In the present experiment '19606' had one of the highest K/Na ratios at 100 mol m^{-3} NaCl under both growing conditions, although its value was lower than 1. 'Sham 1' was the entry with the highest K/Na ratio (also lower than 1) in both hydroponics and sand-culture. In the latter condition, 'Sham 1' had the lowest Na^+ uptake and '19606' the highest K^+ uptake. This entry also showed the least increase of Na^+ at 100 mol m^{-3} NaCl relative to the control treatment (43.1-fold) and the least decrease of K^+ (0.79-fold).

Table 75 shows the concentration of the recorded anions at 100 mol m^{-3} NaCl under both screening methods. Entry differences were significant at $P \leq 0.01$ for NO_3^- and PO_4^{3-} in both conditions, at $P \leq 0.05$ for Cl^- in the hydroponics and at $P \leq 0.10$ for the same ion in the sand-culture. The latter technique had, therefore, a lower capability to discriminate among entries for Cl^- uptake than the hydroponic-culture, similarly to what already observed for the Na^+ concentration. The entries never differed significantly for SO_4^{2-} concentration. Entry '4831' confirmed its possible relative ability to discriminate between Cl^- and NO_3^- (see Table 61), showing also in the present experiment the lowest uptake at 100 mol m^{-3} NaCl of Cl^- and the highest of NO_3^- among all entries. This discriminating ability

Table 75. Entry mean values (± s.e.) and mean separation of the characters chloride (Cl^-), nitrate (NO_3^-), ortophosphate (PO_4^{3-}) and sulphate (SO_4^{2-}) ion concentration (mol m^{-3} expressed sap) recorded on seven durum wheat entries at 100 mol m^{-3} NaCl external in two growing media (hydropon ic-culture and sand-culture). Experiment Bangor 1993.

Entry	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}
	Hydroponic-culture			
S. Cappelli	123.0±5.6 ab	66.5±5.2 abc	80.6±6.0 a	5.3±0.4 a
Sham 1	142.6±12.0 a	34.0±3.3 d	52.1±1.8 b	6.0±0.5 a
19606	143.6±6.5 a	62.2±6.3 bc	50.5±3.2 b	5.2±0.9 a
4831	112.1±7.8 b	87.5±12.3 a	38.2±3.0 c	4.2±1.2 a
17729	137.4±8.1 ab	47.2±5.0 cd	85.2±4.4 a	4.2±0.2 a
38584	144.3±6.5 a	49.3±6.2 bcd	77.4±4.5 a	4.7±1.0 a
5971	120.9±7.7 ab	70.9±6.8 ab	75.5±3.7 a	2.9±0.9 a
	Sand-culture			
S. Cappelli	115.7±10.0 a	60.2±5.8 c	47.9±2.6 abc	4.6±1.1 a
Sham 1	108.1±11.4 ab	51.6±7.2 c	32.3±1.7 cd	6.4±0.7 a
19606	120.2±8.0 a	85.1±4.8 ab	35.7±4.9 bcd	6.1±2.3 a
4831	80.9±9.7 b	104.2±10.1 a	27.8±5.2 d	8.9±1.2 a
17729	108.5±9.1 ab	55.6±9.0 c	54.8±11.2 a	4.3±1.1 a
38584	114.0±4.9 a	69.6±8.4 bc	40.6±4.8 abcd	4.9±1.2 a
5971	111.6±11.3 a	57.3±4.6 c	48.8±1.8 ab	4.1±0.8 a

In each group of means, values followed by the same letter are not different at $P \leq 0.05$ according to Duncan's test.

proved again to be constitutive (see Table 61) as it was also present in the control treatment (data not shown). '4831' was also characterised by the lowest concentration of PO_4^{3-}, confirming the result of the experiment Bangor 1990 (section 7.1.1).

The results of the combined ANOVA are summarised in Table 76. The two screening techniques (hydroponic-culture and sand-culture) differed, on average, only for chloride and orthophosphate ion concentration. The hydroponic-culture had higher content of both these anions. As expected, the two salinity levels differed significantly for all characters. The seven entries were confirmed as a diverse set of materials, their mean values being significantly different for all traits, except for the content of SO_4^{2-} (which was, anyway, by far the least represented ion among those measured).

The interaction between salinity levels and screening techniques was highly significant for shoot and root weight, K^+, Cl^- and PO_4^{3-} concentration. The two salt treatments differed for shoot and root weight only in the sand-culture experiment (Table 77), while the difference between the salinity levels were greater in magnitude for K^+, Cl^- and PO_4^{3-} content in the hydroponic-culture than in the sand-culture (Table 77). In the sand-culture the roots were less affected than the shoots (Table 77). The mean weight ratio between the stress and the control treatment was 0.56 for the shoots and 0.63 for the roots. Munns and Termaat (1986) have reported that in the short-term root growth is less reduced than shoot growth by the stress. The present results indicate that even in a longer time span root growth may be less adversely affected than shoot growth by salinity. The two screening techniques differed significantly both in the control and in the stress treatment for shoot fresh weight, Cl^- and PO_4^{3-} concentration, while they were different for root weight, K^+ content and K/Na ratio only in the stress treatment (Table 77).

In the present study the entries interacted significantly with the screening techniques for both shoot and root weights (Table 76) as was found for the

Table 76. Combined analysis of variance performed on the characters shoot fresh weight (SW), root fresh weight (RW), sodium (Na^+) and potassium (K^+) ion concentration, their ratio (K/Na), chloride (Cl^-), nitrate (NO_3^-), orthophosphate (PO_4^{3-}) and sulphate (SO_4^{2-}) ion concentration of seven durum wheat entries. Experiment Bangor 1993.

		Mean square								
Source of variation	df	SW	RW	Na^+	K^+	K/Na	Cl^-	NO_3^-	PO_4^{3-}	SO_4^{2-}
Technique	1	3.2 ns	0.9 ns	190.6 ns	4174 ns	155.9 ns	6395 **	1388 ns	13002 ***	1.0 ns
Salinity level	1	61.8 ***	8.2 *	1499522 ***	410448 ***	153845 ***	402665 ***	51917 **	24624 ***	146.2 **
Entry	6	8.0 ***	5.1 ***	2574 ***	3727 ***	411.3 ***	1052 **	8424 ***	1708 ***	17.6 ns
Salinity level x technique	1	19.3 **	25.0 **	142.3 ns	17483 **	130.9 ns	3942 **	382.7 ns	1182 *	22.7 ns
Entry x technique	6	2.0 **	1.7 *	596.7 ns	1246 ***	341.6 ***	191.0 ns	1134 ns	232.3 *	18.3 ns
Entry x salinity level	6	1.2 ns	1.0 ns	2521 ***	225.8 ***	395.3 ***	495.1 ns	2138 **	643.6 ***	22.7 *
Entry x sal. level x technique	6	1.0 ns	1.3 ns	552.0 ns	979.9 **	339.3 ***	170.2 ns	1775 **	180.1 ns	27.1 **
Pooled error	141	0.6	0.6	418.6	208.3	63.5	234.2	531.4	90.3	9.0

ns, *, **, *** : not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 77. Comparison of two salinity level (control and 100 mol m^{-3} NaCl) mean values in two growing media (hydroponic-culture and sand-culture), and comparison of the two growing medium mean values at both salinity levels for shoot and root fresh weight per plant, cation concentrations and anion concentrations measured on seven durum wheat entries. Experiment Bangor 1993.

	Hydroponic-culture			Sand-culture			Control	100 mol m^{-3} NaCl
Character	control		100 mol m^{-3} NaCl	control		100 mol m^{-3} NaCl	Hydroponic vs. sand	Hydroponic vs. sand
Shoot fresh weight (g)	3.55	ns	2.99	4.54	***	2.55	*	**
Root fresh weight (g)	2.77	ns	3.16	3.44	***	2.16	ns	***
Na^+ (mol m^{-3} e.s.)[a]	4.2	***	206.8	3.8	***	204.0	ns	ns
K^+ (mol m^{-3} e.s.)	223.9	***	97.2	211.5	***	127.8	ns	**
K^+/Na^+	64.1	***	0.50	67.7	***	0.66	ns	**
Cl^- (mol m^{-3} e.s.)	16.6	***	132.1	13.9	***	108.4	*	**
NO_3^- (mol m^{-3} e.s.)	101.9	*	59.9	104.0	**	69.4	ns	ns
PO_4^{3-} (mol m^{-3} e.s.)	34.8	**	64.8	21.0	**	40.8	**	***
SO_4^{2-} (mol m^{-3} e.s.)	7.3	*	4.7	6.8	ns	5.6	ns	ns

[a] mol m^{-3} expressed sap.

ns, *, **, *** : differences between treatment mean values in each growing medium, or between growing medium mean values at each salinity level, not different, different at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively, according to ANOVA.

weight of the aerial part in the previous comparison of diverse experiments (Table 71). The entry response was, therefore, somewhat experiment-specific and this raises a question about which screening method is the "best" when salt tolerance is assessed in terms of seedling growth.

No interaction between salinity levels and entries was revealed for biomass in the present experiment (Table 76). In all the previously described experiments in which the shoot weight was recorded (viz., Tel Hadya 1989, section 6.2.1.2, Tel Hadya 1990, section 6.2.2.2, and Bangor 1990, section 7.1.1) the 'entry x salinity level' interaction was either non-significant or, at most, significant at 5% probability (Tables 41, 45, 52 and 62). The selection of genotypes for salt tolerance made on the basis of the seedling weight in the stress treatment would mainly be, therefore, a selection for a high growth potential *per se*, i.e., the already mentioned "absolute" tolerance indicated by Rawson *et al.* (1988). The picture would be different if the selection were made on the basis of sodium adsorption. For the concentration of this cation the data analysis showed a highly significant interaction between entries and salt concentrations (Table 76) indicating that the response of the genotypes was different in the control treatment and at 100 mol m^{-3} NaCl.

Neither the shoot weight, nor the root weight at 100 mol m^{-3} NaCl were correlated with the recorded ion concentrations both in the hydroponics and in the sand-culture. A similar result was obtained in the experiment Bangor 1990 with four NaCl external concentrations, from 50 to 200 mol m^{-3} (data not shown).

The experiment Bangor 1993 was carried out at the same time as the laboratory experiment coded as BAN-4 (section 7.2.4). It seemed, therefore, meaningful to correlate the ^{22}Na uptake at low NaCl external concentration (1 mol m^{-3}) of the seven durum wheat entries used in BAN-4 with the Na^+ concentration at 100 mol m^{-3} NaCl of the same entries in the experiment Bangor 1993. Contradicting previous results (see Table 70), in this case the ^{22}Na content of low-salt-grown seedlings proved to be related to the sodium concentration at high salt content. In particular, the correlation coefficient in the hydroponic-culture was $r=0.84$, $P \leq 0.05$, while it was lower (although showing the same trend) in the sand culture ($r=0.61$, $P=0.14$). This finding provides again ground for a possible use of ^{22}Na uptake in low-salt-grown plants as index of sodium adsorption at high NaCl concentration, after that use being doubted by the previous results.

9 *Discussion and conclusions*

Despite its importance as food crop in the area, the productivity of durum wheat in the Mediterranean basin remains low (Srivastava, 1984; Foti *et al.*, 1988). The main reason for low yields is that durum wheat is the food crop grown in the least favourable cropping zones (barley is grown in even more difficult zones, but in all the Mediterranean region this cereal is used exclusively as animal feed). Of the possible factors adversely affecting durum wheat in this area, drought is by far the most important stress (Nachit, 1988). Salinity is another abiotic stress the relevance of which as a constraint to agriculture under arid and semi-arid conditions in the Mediterranean region and elsewhere is increasing at an alarming rate (Szabolcs, 1974; Mashali, 1989).

Plant breeding may represent a means to alleviate the difficulty of durum wheat cultivation in the environment considered. Under dryland conditions, crop improvement will pursue stability of yield, defined as decreased number of crop failures in time, which is of extreme importance in this area due to erratic and unpredictable climatic conditions from season to season (Ceccarelli *et al.*, 1987a). An understanding of the mechanisms underlying drought resistance is essential, in order to assess which traits could be used in addition to grain yield to increase selection efficiency. By means of this strategy the desirable integration between the two possible selection approaches (empirical and analytical) could be attained (Ceccarelli, 1987).

In the case of salinity stress, breeding of resistant materials will be more efficient if a 'pyramiding' approach is adopted (Yeo and Flowers, 1986), that is, the integration of useful traits identified by different screening methods. Variation for salt tolerance in the existing cultivars may be exploited and the selected lines used as a basis for further breeding. However, of the most commonly grown winter cereals durum wheat is the most susceptible to salinity (Gorham *et al.*, 1990a) and the range of tolerance within commercial varieties is very restricted. Greater variation may be sought in unimproved landraces and in related wild species (Sayed, 1985; Nevo *et al.*, 1992, 1993).

A key of successful breeding for low-yielding, stressful conditions is the use of adapted germplasm (Ceccarelli and Grando, 1991). Usually the most adapted germplasm is the one that has been able to co-evolve with the environment in which it grows. This is the case of the so-called 'genetic resources', which include landraces, primitive cultivated species, wild progenitors and other wild species (Frankel and Hawkes, 1975). Landraces, in particular, may possess adaptive genetic complexes associated with the special conditions of cultivation, which may be of great interest for plant breeding. The results reported in the abundant bibliography mentioned in section 1.4 of this thesis indicate that genetic resources are a reservoir of readily available genetic variability which can be used in breeding for tolerance to abiotic stresses. Landraces may be used either directly through mass selection of pure lines (Ceccarelli *et al.*, 1991), or indirectly utilizing the best selections for specific traits as parents in crosses with either other selections from landraces or introduced germplasm (Srivastava, 1987).

The present study was aimed at investigating several facets of durum wheat improvement for drought and salinity resistance in the Mediterranean region. The purpose of such an effort was two fold. On the one hand, it assessed the role of the genetic resources as a possible source of adaptation to the stress conditions in the target area. On the other hand, the study assessed the importance of several morpho-physiological traits as tools to enhance crop improvement for the two stresses.

It is hoped that this thesis may be helpful to whoever is dealing with the problem of drought and salinity stress in durum wheat, at least by throwing some light on certain aspects of the matter, and that the findings here reported may be added as a brick, however small, to the wall of selection against these two major agriculture constraints.

9.1 *Drought*

The results of field trials conducted both in Syria and Sicily provided evidence that durum wheat landraces may contain interesting materials in terms of adaptation (high and stable yield) to dryland conditions. Interesting accessions were found under both the severe stress conditions of Breda (Syria) and the generally more favourable conditions of Libertinia (Sicily). In this, the present investigation confirmed the interest raised by landraces in a large part of the breeding community around the Mediterranean, as possible donors of positive attributes. Different breeding programmes aim at combining the favourable adaptive features of landraces with the high yield potential of modern genotypes: e.g., in Jordan (Duwayri *et al.*, 1987), in Sicily (Boggini *et al.*, 1990), and in Tunisia (Daaloul *et al.*, 1990). Given the wide year-to-year precipitation fluctuations typical of the region, this strategy seeks to obtain varieties with a high level of yield stability to prevent crop failures in the unfavourable seasons and ensure satisfactory yields in the more favourable seasons (Srivastava, 1987).

Selection for grain yield proved to be rather season-specific, due to the occurrence of a strong genotype x season interaction. Nonetheless, it was possible to identify some lines which were able to perform well in more than one season. In a few cases there appeared to be genotypes ranking among the best at both localities, such as the Jordanian landrace '83089'. For this and for the other entries with similar behaviour, a good adaptation across the Mediterranean basin is likely.

If one of the aims of breeding is to broaden the genetic base and, hence, improve the adaptation of the varieties presently available (Boggini *et al.*, 1992), the genotypes identified as high and stable yielding could certainly be suitable for the purpose.

To some extent, the selection made in Syria also seemed effective for the Sicilian area. It has been shown for barley (Ceccarelli and Grando, 1991) and durum wheat (Pecetti *et al.*, 1992b) that some materials selected under unfavourable conditions are able to retain their superiority in a more favourable environment.

The Jordanian gene pool was confirmed to be a source of valuable germplasm under Mediterranean conditions (Pecetti and Annicchiarico, 1991).

Variability of the tested materials proved very high for most of the traits under evaluation in all environmental conditions. Variability may be very desirable in breeding activities for drought tolerance. If the objective was to evaluate and validate the potential of a trait, Richards (1989) stated that testing a substantial number of diverse genotypes would be an alternative to the use of near-isogenic lines. The diversity of the materials under test avoids bias of trait verification associated with the specific nursery used (Acevedo and Ceccarelli, 1989).

As regards the assessment of the potential traits to enhance the selection of durum wheat germplasm for drought tolerance, the results obtained under severe conditions have confirmed the role of stress escape mechanisms such as earliness to ensure good yields. The importance of earliness for good performance of durum wheat under moisture-limiting conditions has been repeatedly indicated (e.g., Fischer and Maurer, 1978; Acevedo, 1991; Annicchiarico and Pecetti, 1993). Morgan (1989) and Richards (1989) saw the development of faster maturing types as the basic drought escape mechanism to better match the water demand to water supply. This implies modifying crop phenology so that the most sensitive growth periods avoid the most severe stress periods. Harris *et al.* (1987)

stated that early cultivars are best suited to drier sites with less than 350 mm rainfall. As the heritability of flowering time is usually high, and the character is easily assessed, earliness of flowering is a character which can be easily bred for (Bidinger and Witcombe, 1989).

At Breda, a long peduncle was also a feature consistently associated with a high yield. As it was not correlated with earliness (and, hence, stress escape), peduncle length is most probably an indicator of some tolerance mechanism(s). Nachit and Jarrah (1986) found that durum wheat lines differing in peduncle length also differed in tillering capacity and grain yield under dry conditions. It may be inferred that maintenance of a long peduncle must be related to the ability to withstand drought stress as elongation of this internode occurs in Mediterranean conditions invariably during a phase of declining rainfall. Maintenance of elongation of shoots (and roots) could be attained with maintenance of positive turgor through osmotic adjustment (Morgan, 1989).

Given the high incidence of frost days during winter and the likelihood of late frosts in northern Syria (section 2.1), it was not surprising to see that frost tolerance was also related to good performance at Breda. In both seasons of evaluation at this locality frost events were associated with severe drought. This confirmed to be a distinct feature of northern Syria (Acevedo, 1987). However, from a breeding point of view it would be interesting to separate the effect of the two stresses and "quantify" how drought tolerant *per se* and how frost tolerant *per se* are the identified best materials.

In Syria the number of kernels per spike was the yield component mostly related with grain yield, confirming previous results of Annicchiarico and Pecetti (1993) and Simane *et al.* (1993) in the same environment. It is possible that the higher spike fertility of the best genotypes under very dry conditions at Breda originates from better stress tolerance. Morgan (1980) and Richards (1987) have advocated osmotic adjustment as a mechanism to improve seed setting under drought. Very recently, a strong positive association has been found under moisture stress between $\Delta^{13}C$ and number of kernels per spike (Morgan *et al.*, 1993). These authors concluded that genotypic variation in $\Delta^{13}C$ reflects plant metabolic traits that influence yield primarily through effects on grain number.

All three yield components (spike number, spike fertility and kernel weight) contributed to high yields at Libertinia. The generally better conditions in Sicily relative to Syria enable a higher yield potential, which is obtained through a larger "sink" capacity and better kernel filling. Only in the most unfavourable season at Libertinia was there a positive effect associated with early heading, confirming that the more stressful are the growing conditions, the more useful is the stress escape mechanism.

9.2 *Crop modelling*

Novel agronomic techniques such as dynamic crop growth models seem applicable in dry Mediterranean environments. Such models provide a realistic approach to the genotype x environment (including soil and climate) interaction over the entire life of the crop. Genotype adaptation and productivity can be well defined in the target area by using long-term historical weather data records, provided, of course, that climatic change will not occur too rapidly and, hence, historical data will also be trends for the future. Such models could have a great impact on the definition of the "ideotype(s)" for the considered conditions, and could assist in the choice of parental materials (McWilliam, 1989). For this purposes, a user-specified definition of certain traits should be implemented. Priorities should be assigned to adaptive traits that have the greatest effect on the crop's response to water stress. It would be of interest, for instance, to try to "weigh" the importance in terms of performance of easily measured characters which are thought to be related to the yield response under dryland conditions, such as peduncle length, awn size, or flag-leaf size. Richards (1989) suggested that modelling may detect the impact of a changed expression of a trait or a particular combination of traits on the growth and yield of a crop in different seasons, and establish a priority list of traits to develop into suitable genetic material for field testing.

The CERES-Wheat crop model used in this study permitted alteration of the phenology of the genotypes studied. The results highlighted the importance of earliness and of duration of the grain filling to improve the simulated yield. The date of sowing was a factor markedly influencing the simulated performance of genotypes. Delaying of sowing resulted in decreased yield, the maximum yield being obtained with sowing at the beginning of November. The results fully confirmed those of Stapper and Harris (1989) also obtained for the Mediterranean region. It seems advisable to carry out the sowing as soon as possible after the onset of the rainy season (reasonably between 1 and 15 November). In a location characterised by likelihood of late frosts (such as Breda) the adoption of an early variety for early sowing may present serious risks of frost damage during sensitive phases of the cycle. In this case, a genotype with medium earliness should be preferred. The results also indicated that under very dry conditions it may be at an advantage to sow soon after a rainfall event. Even a small early increase of soil water content will result in most cases in higher yields.

Observations on a simulated water stress factor at various growth stages showed that at Breda stress between the end of ear growth and the beginning of grain filling may affect very adversely final yields. Actual data support the finding that a drought stress applied at flowering is more detrimental to grain yield than a stress applied either at tillering or during grain filling (Simane *et al.*, 1993). This stage is considered to have a major impact on the number of grains per spike (Ritchie, 1991). This could be a reason for the great importance that spike fertility has on discriminating the most adapted germplasm in the environment (Annicchiarico and Pecetti, 1993; Simane *et al.*, 1993; Table 9 in this thesis).

It appeared that the CERES-Wheat model, developed for more favourable conditions, should be modified and better calibrated for the considered area as regards the simulation of extreme conditions, both favourable and unfavourable. An estimation of frost damage, particularly of late events, for all wheats, and of lodging damage under excessive late rainfall, for durum wheat, should be provided.

9.3 *Osmotic adjustment*

Of the physiological traits advocated as stress tolerance mechanisms, one of the most cited is osmotic adjustment (e.g., Morgan (1989), Al-Dakheel (1991), and the literature reviewed by both authors). In the present study the ability to adjust osmotically was sought in durum wheat seedlings artificially exposed to drought stress during their first days of development, following the procedure suggested by Morgan (1988). The results showed that one genotype ('83089'), possibly stress tolerant under field conditions, seemed to possess the ability to adjust osmotically and maintain turgor. In contrast, another genotype possibly adapted to field stress ('17870') had the lowest turgor pressure under this artificial stress. Quite unexpectedly, the entry with osmotic adjustment ('83089') had the smallest growth during stress imposition, while '17870', certainly not adjusting, showed the largest growth under stress. The results did not agree with those of Morgan (1988) and Blum (1989) who found differences in osmotic adjustment between genotypes (of bread wheat and barley, respectively) which were consistent with differences in coleoptile growth under stress. Entry '17870' showed the least reduction of leaf water potential relative to the watered control. This result might indicate a possible drought "avoidance" in the sense of ability to endure periods of drought whilst maintaining a high plant water status (Levitt, 1972). The two entries with interesting field performance under drought stress showed therefore substantially contrasting physiological mechanisms. It would seem that their good adaptation to drought is due to either stress tolerance ('83089'), or avoidance ('17870'). That implies, of course, that the osmotic adjustment shown at the seedling stage by '83089' is somewhat positively related to its behaviour at the adult stage, in spite of its negative relationship with the growth at the seedling stage. It might be worth verifying the water status of both entries under actual field conditions and relate the findings there obtained with those of the present study.

The results in this experiment were inconsistent with respect to previous results in similar experiments, and to observed genotype behaviours under real conditions. This suggests some caution in the adoption of osmotic adjustment ability in the early stages of ontogeny as a selection criterion to identify the best durum wheat genotypes under field drought stress.

9.4 *Salinity*

Selection for resistance under naturally occurring saline stress seemed unreliable from an experimental point of view, though it is certainly more realistic than any other selection approach. Due to the patchy occurrence of salt throughout the field, it was very difficult to distinguish between really tolerant accessions and accessions just growing on salt-free spots. The situation observed at Hegla, northern Syria, is common in all heavily salt-affected fields (Richards 1983b). In this sense, it seems sound to accept Richards'(1983b) argument that the best breeding strategy for improving the overall yield of crops growing on such fields is to select for high yields on non-saline soils. His assumption was based on the observation that most of the yield in a field will come from the least saline patches, and that selection for yield in non-saline soils is easier to achieve than any selection for salt tolerance. Moreover, it is likely that introducing resistance mechanism(s) into a genotype would result in a decreased yield potential under non-saline conditions.

If, nonetheless, genotype selection is to be pursued under saline conditions, with the aim of obtaining tolerant varieties in the presence of stress, the spatial (and temporal) variability inherent in saline soils (Richards, 1983b) should be avoided. Large experimental errors reduce the power of statistical tests and hinder discrimination on the basis of such tests. Uniformly salinized soils may be unobtainable unless synthesized, which then may cause the problem of cost for large scale evaluations. Francois *et al.* (1986) and Aragüés *et al.* (1992) obtained controlled field salinity conditions by irrigating field plots with salinized water. In both cases the number of genotypes tested was limited. To avoid the variability encountered in field screening and control the salt levels, plants are often grown in nutrient solution to which salt is added, adopting survival and/or early growth rather than grain yield as indicators of stress resistance (McGuire and Dvorák, 1981; Sayed, 1985; Kingsbury and Epstein 1986, 1988; Rawson *et al.*, 1988).

In the present research, screening of durum wheat genetic resources under saline conditions was made under artificially induced stress in controlled environments. The experiments here described have adopted the seedling weight (in most cases shoot weight) as the parameter to assess the salt tolerance of durum wheat entries. According to Rawson *et al.* (1988) early measurements of biomass production were largely in accord with the documented reputations of the tested genotypes for salt tolerance under real conditions. Sayed (1985) stated that tolerance at early stages was a reliable indication of tolerance at maturity, and the interpretation of results from early stages of development appeared valid for late stages.

The unrelatedness shown in this study (see section 8.2) between seedling weight and the content of the main ions involved in the salt stress raises a question about the reliability of seedling weight as an indicator of salt tolerance. It is possible that the decrease of plant weight is dependent more on the buildup of salt in the oldest leaves (Munns and Termaat, 1986) than on the salt accumulation in the youngest leaf (the one measured in these experiments). Low carbohydrates reserves caused by stuntedness or even death of oldest leaves may indeed adversely affect growing regions (Munns and Termaat, 1986). Salt concentrations at a given time of exposure to salinity are always highest in oldest leaves (Greenway and Munns, 1980). Under these assumptions, plant weight could still be a valid parameter of salt tolerance, even in the absence of a strong relationship with the salt concentration in the youngest leaf.

Different experiments were carried out under different experimental conditions. Plants were grown either on a sand substratum to which the nutrient solution was added, or in hydroponics. The data obtained have indicated that different growing conditions might lead to conclusions which are not fully consistent. The differences between methods are certainly greater when these methods are adopted under very different environmental conditions in terms of radiation, temperature, etc. Even when the evaluations are carried out under the same conditions (such in the experiment Bangor 1993) there is a significant interaction between the entries and the screening techniques. Some entries have shown somewhat similar responses in sand-culture experiments, even when carried out under different external conditions. For instance, there was some consistency of behaviour for '4831' and 'Sham 1' in the three experiments Tel Hadya 1989, Tel Hadya 1990 and Bangor 1993, and for '19606' in the two cases in which it was evaluated (Tel Hadya 1990 and Bangor 1993). On the other hand '5971' and '38584' did not confirm in other trials the outstanding performance shown in Tel Hadya 1989 and Tel Hadya 1990, respectively. In general, it could be concluded that the entry response to the salt stress was rather experiment-specific. This finding may have important experimental consequences, as wide verification would be needed to assess which evaluation environment is the best for selection. Based on the present results it is difficult to say which method is advisable. The analysis of variance at high salinity concentration (100 mol m^{-3} NaCl) has provided a rough solution to the problem. Sand-culture appeared somewhat more useful to separate entries on the basis of their seedling growth, while hydroponic-culture seemed a little more sensitive in the detection of differences among entries for their ion accumulation (in the youngest leaf) under stress. Hydroponic-grown plants have showed signs of stunted growth (particularly of the roots) independent of the presence of the salt stress. Root development and the environment experienced by the roots in hydroponics may be very different from those found in the field (Hollington *et al.*, 1992), while the relationships between sand-culture conditions and field conditions might be worth further assessment.

There have been indications in this study that the 'genotype x salinity level' interaction for seedling weight is seldom strong (at least up to levels of 100 mol m^{-3} NaCl). The implication of this finding from an experimental point of view is that the selection for an "absolute" growth ability (in the absence of the stress) should also allow the selection of the genotypes with the best growth in the presence of the stress, as already expressed by Rawson *et al.* (1988).

If stress tolerance is assessed on the basis of morpho-agronomic traits (such in the experiment Tel Hadya 1989, final harvest), the interaction between genotypes and salinity levels may be very strong for characters such as days to heading, number of tillers per plant, leaf area and dry matter per plant (Table 46). Entry ranks may be very different in the control and in the stress treatment. Nonetheless, examining wild wheat genetic resources (experiment Tel Hadya-wild, section 6.2.3.2) the genotype x salinity level interaction was not significant for traits such as number of tillers per plant and days to heading (Table 55). The interaction was not significant in either cultivated or wild materials for characters such as number of leaves and plant height (Tables 46 and 55).

As regards selection of promising materials to be used in breeding programmes, the results concerning salinity were somewhat less rewarding than those obtained for drought tolerance. Variability does exist within genetic resources (including some wild relatives of cultivated durum wheat), but there did not appear to be any source of significantly better tolerance to this stress, at least to high salinity levels. There seemed to be an upper salinity limit to stress tolerance at an adult stage. This limit lies between 100 and 150 mol m^{-3} NaCl, beyond which none of the tested durum wheat entries survived to completion of the growth cycle. This salt concentration corresponds to an electrical conductivity of about 11-14 dS m^{-1} (Wyn Jones and Gorham, 1986; sections 6.2.1.2 and 6.2.2.2 in this thesis). These experiments seemed more adverse for the species than the natural conditions described by Richards (1983b). In his experiment a conductivity (EC_e) of 13 dS m^{-1} would cause an estimated reduction of 57% grain yield, while in the present study at that stress level there wouldn't simply be any yield because of death of the plants.

Previous results (Sayed, 1985) suggest that screening of thousands of accessions is perhaps needed to find "tolerant" genotypes. It cannot be excluded, however, that the set of accessions evaluated in the present study was, on the whole, less tolerant than the one screened by Sayed (1985).

Some entries were noted for their relatively better tolerance than other tetraploid lines. These genotypes (for instance, landraces '19606' from Syria and '3772' from Ethiopia, the cultivar 'Sham 1', and the accessions 'DICSNS157', 'DICSNS197' and 'DICSNS410' of *Triticum dicoccoides*) deserve further assessment of their behaviour under salt stress, possibly under more "realistic" conditions (e.g., under controlled field salinity, such as those mentioned in section 6.1), in order to verify the relationship between the data obtained in the present study and those under "real" conditions. If confirming their "relative" tolerance, they should be used for breeding. For instance, they could act as recipient for the introgression of identified resistance mechanisms, such as the enhanced K/Na discrimination trait present in the diploid and hexaploid, but not in the tetraploid wheats (Gorham, 1993). As already reported, recombinant lines which contain the gene controlling this character have been obtained from the durum wheat variety 'S. Cappelli'. This old variety has outstanding agronomic characteristics for the semi-arid areas (see section 1.4), but it has also proved of some interest in these salinity-related experiments, at least with NaCl levels not exceeding 100 mol m^{-3}. 'S. Cappelli' seems to combine a high growth rate with a modest reduction of growth under stress relative to the control treatment (sections 6.2.1.2 and 8.2). Similar characteristics, but to an even greater extent, were shown by '19606' for which a combination of both an absolute (intrinsic high growth rate) and a physiological tolerance to salinity (Rawson *et al.*, 1988) could be postulated. This entry also showed other positive features such as a relatively (to other tetraploid accessions) higher potassium concentration and a relatively lower sodium concentration in the presence of the salt stress. Its K/Na ratio was 3.46 at 50 mol m^{-3} NaCl (Table 65) and higher than that of other durum wheat entries at 100 mol m^{-3} NaCl (Table 74). Gorham *et al.* (1991) suggested that at 50 mol m^{-3} NaCl external concentration a K/Na ratio greater than 2.5 might be taken to indicate the presence of the enhanced K/Na discrimination character.

To some extent, the modern variety 'Sham 1' also seemed to possess important characteristics for salt tolerance. Its response to salinity levels up to 100 mol m^{-3} NaCl was relatively little affected compared to the control treatment. In the experiment Bangor 1993 (section 8.2) it showed the least increase of Na^+ concentration at 100 mol m^{-3} NaCl relative to the control treatment (among seven durum wheat entries) in hydroponics, and it had the highest K/Na ratio both in the hydroponics and in the sand-culture (Table 74). A constant feature of this cultivar under the adopted growing conditions was its rather poor growth potential. It must be noted that 'Sham 1' is characterised under field conditions by outstanding agronomic features, which make it one of the most promising varieties in the Mediterranean region (Pecetti and Annicchiarico, 1993).

At the species level there is a good correlation between enhanced K/Na discrimination and ^{22}Na accumulation in low-salt-grown seedlings (Gorham, 1993). In this study, some tests were carried out on durum wheat entries under the hypothesis that any difference in sodium accumulation at high salinity, indicating possibly different K/Na discrimination, could be related to different ^{22}Na uptake at low salt concentration. Measurements of the radioisotope ^{22}Na at low NaCl external concentration revealed a great variation among durum wheat genotypes for this trait. However, inconsistent results were obtained on the relationships between ^{22}Na concentration in low-salt-grown seedlings and sodium adsorption at high salinity levels. Most of the tests suggested that ^{22}Na uptake into low-salt-grown seedlings is not necessarily closely correlated with Na leaf concentration at higher salinity. To some extent, the adsorption of ^{22}Na at low salt concentration seemed biased by the leaf size of the genotypes, in spite of the fact that the character was measured on the basis of the same unit weight (section 7.2.1). It cannot be excluded, however, that the relationship between ^{22}Na uptake and leaf size is simply a consequence of the simultaneous presence in the Ethiopian landraces of very small leaves and very low levels of ^{22}Na without the two traits being biologically related. It is difficult to explain the relationship observed between an attribute considered to be negative such as high ^{22}Na uptake at low salt concentration, and a feature which is considered positive such as high potassium content at higher salinity concentration (Table 70). It is similarly incongruous that entry '19606', which was one the most tolerant durum wheat genotypes at high salt concentrations (up to 100 mol m^{-3} NaCl), had a high ^{22}Na adsorption at low NaCl external concentration (section 7.2.1). These results suggest little usefulness of

^{22}Na measurements to discriminate durum wheat genotypes for their salt tolerance. However, the results of the experiment Bangor 1993 (section 8.2) have shown that in some cases a certain prediction of sodium uptake at high salinity on the basis of ^{22}Na content at low salt concentration may occur. The possible use of ^{22}Na as an index of intra-specific variability in durum wheat for sodium uptake under salt stress remains, therefore, uncertain.

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TEXT CUT OFF IN ORIGINAL THESIS

Table 5. Summary of the analysis of variance of 25 selected (on the basis of their agronomic score) durum wheat entries for the characters recorded at Breda in 1988-89 and 1989-90.

1988-89

Character	Grain yield	Early vigour	Frost damage	Days to heading	Plant height	Days to maturity	Peduncle length	No. of tillers	Spike length	No. kernels per spike	1000-kern. weight
F-test significance	*	***	*	***	**	***	ns	*	**	ns	***

1989-90

Character	Grain yield	Early vigour	Frost damage	Days to heading	Plant height	Days to maturity	Peduncle length	No. of tillers	Days to emergence
F-test significance	***	ns	***	***	***	***	ns	***	**

ns, *, ** and ***: not significant, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Table 20. Accession number and grain yield per plant of the best yielding entries (out of 75 entries) in three seasons of evaluation at Libertinia.

Accession number	Grain yield per plant (g) 1990-91	 1991-92	 1992-93
83089	23.6	12.8±1.4	8.5±1.8
7598	23.0	-	-
7178	21.1	-	-
83008	20.6	12.8±3.8	8.6±0.2
7237	17.8	10.4±1.3	-
7788	17.1	15.8±2.6	-
4727	16.8	11.0±1.2	9.6±2.7
37565	16.6	10.6±0.1	8.0±0.9
6617	16.5	10.8±1.3	-
83005	16.3	11.7±1.3	10.4±3.3
9245	16.3	-	-
6614	-	16.6±3.3	-
6834	-	15.5±2.1	-
9705	-	15.4±3.4	-
6748	-	14.5±4.3	-
9408	-	14.3±1.3	-
6882	-	13.9±1.8	-
6974	-	13.3±3.9	-
7710	-	13.3±4.3	-
7805	-	13.0±1.4	-
5695	-	12.9±2.3	-
6657	-	12.8±2.6	-
7736	-	12.6±1.5	-
83022	-	12.4±3.8	7.7±1.7
6822	-	11.9±1.2	-
7419	-	11.7±1.7	8.5±1.8
7827	-	11.5±1.2	-
M13	-	11.4±1.3	-
37499	-	11.2±1.4	10.3±2.0
7688	-	11.1±3.1	-
7274	-	10.9±2.6	-
7754	-	10.9±2.3	-
6674	-	10.9±1.3	7.2±1.8
7539	-	10.7±0.1	-
6838	-	10.7±0.8	-
7638	-	10.6±0.9	8.4±0.9
6702	-	10.5±1.3	-
7781	-	10.3±2.5	-
6821	-	10.3±1.5	-
83063	-	-	11.2±2.4
7833	-	-	10.6±0.8
12257	-	-	9.4±1.7
10926	-	-	7.9±1.1
M21	-	-	7.6±1.5
5971	-	-	7.5±1.1
9282	-	-	7.3±2.1
7331	-	-	6.9±1.6
38552	-	-	6.8±0.4
7267	-	-	6.7±1.6
Mean	18.7±0.8	12.2±0.3	8.5±0.3

Yield values in 1990-91 did not differ from each other at P ≤ 0.05 according to LSD calculated for the modified augmented design; in 1991-92 and 1992-93 yields did not differ at P ≤ 0.05 according to Duncan's test.

Table 30. Simple correlation coefficients between simulated grain yield and an estimated water stress factor affecting leaf expansion and growth at various stages of growth and averaged across stages for three sowing dates at two locations.

Location	Stage of occurrence of estimated water stress	Sowing date[a]		
		1 November	26 November	20 December
Breda	Terminal spikelet initiation to end of vegetative growth and beginning of ear growth (stage 2)	-0.47 *	-0.38 @	-0.43 *
	End of vegetative growth and beginning of ear growth to end of pre-anthesis ear growth (stage 3)	-0.68 **	-0.44 *	-0.25 ns
	End of pre-anthesis ear growth to beginning of grain filling (stage 4)	-0.89 **	-0.85 **	-0.87 **
	Linear grain filling (stage 5)	-0.70 **	-0.57 **	-0.66 **
	Across previous stages (average)	-0.87 **	-0.73 **	-0.68 **
Libertinia	Stage 2	-0.33 ns	0.21 ns	-0.06 ns
	Stage 3	-0.62 *	-0.16 ns	-0.33 ns
	Stage 4	-0.78 **	-0.40 ns	-0.72 **
	Stage 5	-0.68 **	-0.92 **	-0.80 **
	Across previous stages (average)	-0.89 **	-0.63 *	-0.70 **

[a] across cultivars.

ns, @, *, ** : not significant, significant at P<0.10, P<0.05 and P<0.01, respectively.

Table 31. Mean values across seasons and cultivars of an estimated water stress factor (0 = min, 100 = max) affecting leaf expansion and growth at various stages of growth and averaged across stages for thre sowing dates at two locations. For growth stage definitions see Table 30.

Sowing date	Water stress factor at									
	Stage 2		Stage 3		Stage 4		Stage 5		Mean of all stages	
	Breda	Libertinia	Breda	Libertinia	Breda	Libertinia	Breda	Libertinia	Breda	Libertini
1 November	24.0	0.4	57.4	22.2	78.5	49.6	87.7	62.8	61.9	33.8
26 November	27.9	19.0	72.6	46.2	81.3	45.1	92.9	80.1	68.7	47.6
20 December	29.4	31.2	72.4	49.2	86.4	60.8	94.4	84.6	70.7	56.5

Table 56. Entry mean values of seven morphological traits recorded in the control treatment (con) and at 100 mol m^{-3} NaCl external concentration (100). Experiment Tel Hadya-wild.

	Number of tillers[1]		Number of leaves		Days to heading		Peduncle length (cm)		Plant height (cm)		Number of spikes		Number of spikelets	
Entry	con	100	con	100	con	100	con	100	con	100	con	100	con	100
BONSN135	14.0 a	15.9 ab	7.1 a	6.4 a	109.9 a	109.0 a	4.5 a	3.1 a	14.9 a	11.1 a	1.6 a	1.6 a	11.2 a	10.0
BONSN140	19.1 a	17.1 ab	6.5 a	6.7 a	111.4 a	109.9 a	4.7 a	3.3 a	13.0 a	10.9 a	1.7 a	1.7 a	11.5 a	10.0
BONSN160	13.2 a	9.9 b	7.1 a	7.5 a	-	-	-	-	-	-	-	-	-	-
BONSN204	12.2 a	11.5 ab	7.0 a	6.7 a	111.7 a	110.9 a	4.5 a	2.9 ab	13.4 a	10.7 a	1.6 a	1.4 a	10.2 a	9.2
BONSN296	15.7 a	18.1 a	7.2 a	6.5 a	110.4 a	109.0 a	3.8 b	2.5 b	14.6 a	10.7 a	2.1 a	1.5 a	11.1 a	8.5
Mean *T. boeoticum*[2]	14.9 ns	14.5	7.0 ns	6.8	111.1 *	109.9	4.4 ***	2.9	14.0 ***	10.8	1.8 ns	1.6	11.0 ***	9.4
DICSNS157	10.5 b	9.4 b	7.6 b	6.6 c	101.2 b	101.6 a	51.4 a	47.2 a	100.6 a	88.9 a	5.0 a	5.1 a	13.5 a	11.1
DICSNS165	19.2 a	21.1 a	8.1 ab	7.9 b	-	-	-	-	-	-	-	-	-	-
DICSNS173	19.9 a	23.7 a	8.2 ab	7.7 b	-	-	-	-	-	-	-	-	-	-
DICSNS197	10.2 b	13.0 b	9.0 a	8.5 ab	111.2 a	108.7 a	16.1 b	12.9 b	67.1 b	62.7 b	2.7 b	2.7 b	13.4 a	13.0
DICSNS410	18.6 a	24.2 a	9.2 a	9.1 a	-	-	-	-	-	-	-	-	-	-
Mean *T. dicoccoides*[2]	15.7 ns	18.3	8.4 ns	8.0	104.8 ns	104.1	33.7 ns	30.1	83.9 ns	75.8	3.9 ns	3.9	13.4 ns	12.1
S. Cappelli[2]	4.5 ***	2.7	7.7 ns	7.6	97.2 ns	100.9	48.9 ***	41.1	99.2 *	81.5	2.2 *	1.5	14.0 ns	12.1
Mexipak[2]	4.6 ns	3.0	6.0 ns	6.6	76.7 ns	71.7	32.7 ns	30.9	78.0 ns	73.7	4.0 *	2.2	16.2 ns	15.2

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[1]: entry means followed by the same letter in each salt treatment within each wild wheat species are not different at P 0.05, according to Duncan's multiple range test.

[2] ns, *, *** : means in the two salt treatments not significantly different, different at $P \leq 0.05$ and $P \leq 0.001$, respectivel according to ANOVA.

Table 70. Correlation coefficients (r) among cation concentrations measured in durum wheat shoots entries grown in different laboratory experiments at Bangor. The figures in parentheses beneath each value represent the number of entries in common within each pair of experiments. For trait abbreviatio and experiment codes see section 7.2.5.

	^{22}Na BAN-2$_{(1:1)}$	^{22}Na BAN-2$_{(25:1)}$	^{22}Na BAN-3	^{86}Rb BAN-3	^{22}Na BAN-4	Na Dur-2	K Dur-
^{22}Na BAN-1	0.83 *** (13)	-0.05 ns (13)	-0.36 ns (13)	0.81 *** (13)	0.68 @ (7)	-0.10 ns (17)	0.59 (17)
^{22}Na BAN-2$_{(1:1)}$	-	0.03 ns (13)	-0.16 ns (13)	0.64 * (13)	nc	-0.15 ns (9)	0.73 (9)
^{22}Na BAN-2$_{(25:1)}$		-	-0.15 ns (13)	-0.13 ns (13)	nc	0.00 ns (9)	-0.17 n (9)
^{22}Na BAN-3			-	-0.64 * (13)	nc	0.26 ns (9)	-0.29 n (9)
^{86}Rb BAN-3				-	nc	-0.11 ns (9)	0.58 @ (9)
^{22}Na BAN-4					-	nc	nc
Na Dur-2						-	-0.04 n (17)

nc : not computed because of too few entries in common between the two experiments.
ns, @, *, *** : not significant, significant at $P \leq 0.10$, $P \leq 0.05$ and $P \leq 0.001$, respectively.

Table 74. Entry mean values (± s.e.) and mean separation of the characters sodium (Na^+) and potassium (K^+) ion concentration (mol m^{-3} expressed sap), and their ratio (K/Na) recorded on seven durum wheat entries at 100 mol m^{-3} NaCl external concentration in two growing media (hydroponic-culture and sand-culture), and ratio between the mean Na^+ and K^+ concentration at 100 mol m^{-3} NaCl and that in the control treatment in both media. Experiment Bangor 1993.

	Na^+	K^+	K/Na	Na^+ (100 mol m^{-3} NaCl : control)	K^+ (100 mol m^{-3} NaCl : control)
	Hydroponic-culture				
S. Cappelli	211.9±14.9 ab	99.1±9.4 ab	0.49±0.06 abc	54.3	0.46
Sham 1	176.3±7.6 c	120.4±14.1 a	0.70±0.10 a	36.9	0.49
19606	186.1±8.0 bc	116.8±7.2 a	0.64±0.07 a	53.2	0.54
4831	173.9±8.9 a	104.7±6.5 a	0.60±0.04 ab	48.3	0.49
17729	239.8±6.3 a	67.3±4.2 b	0.28±0.02 c	43.6	0.28
38584	243.7±11.7 a	70.1±7.4 b	0.30±0.04 c	62.5	0.35
5971	227.1±9.6 a	88.0±12.1 ab	0.40±0.07 bc	61.4	0.39
	Sand-culture				
S. Cappelli	215.4±16.2 a	118.4±14.8 b	0.58±0.10 b	43.9	0.49
Sham 1	171.4±17.0 b	142.4±17.3 ab	0.91±0.17 a	59.0	0.66
19606	193.8±14.1 ab	172.9±19.2 a	0.91±0.09 a	43.1	0.79
4831	203.0±10.7 ab	121.4±12.3 b	0.60±0.06 ab	59.7	0.68
17729	211.1±13.3 ab	125.9±11.0 b	0.62±0.09 ab	54.1	0.59
38584	211.7±8.5 ab	105.2±15.3 b	0.51±0.09 b	57.2	0.51
5971	222.7±7.3 a	107.9±12.8 b	0.49±0.07 b	69.6	0.52

In each group of means, values followed by the same letter are not different at $P \leq 0.05$, according to Duncan's test.