

AGRONOMIC TRAITS USEFUL IN SUNFLOWER BREEDING FOR DROUGHT RESISTANCE

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SUMMARY

During last 20 years, crops of sunflower have extended throughout the developing countries due to its capacity to adapt to dry environments. Although a plant moderately tolerant of drought, production from this oil crop is strongly influenced by the presence of water stress which is found fairly regularly.

In fact, drought is a permanent feature in many developing countries and may also periodically influence the economies of Europe and the USA.

The threat from the trends in the global climate render this property ever more important.

At a scientific level there is a mass of work on the relationship between water supply and plant yield, but most deal with crops under irrigation. In contrast, useful knowledge concerning the improvement of the species to environments with trophic, especially water, limitations are still scarce and fragmentary. In our paper we have attempted to establish the state of the art of research into the strategies to adopt for improving drought resistance in sunflower, whilst trying to identify which of the many agronomic factors and physiological parameters may be used to improve the efficiency of selection processes.

In the establishment of a genetic improvement program aimed at improving the resistance to water stress, the following points must be included:

1) define the types of drought environment encountered in the target environment for each plant breeding program, because different types of drought may require different approaches.

2) describe plant "ideotypes" once the target environment is accurately defined.

3) determine which traits are to be considered to assist the development of drought-resistant cultivars.

4) given the particularly difficult conditions and unusual nature of drought-prone environments, accuracy is required in the identification of the selection method and the conduction of the experiment, in an attempt to steer the choice (identification of better progeny) towards data with a high number of replicates and not just single values.

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5) analysis of data which allow the interpretation of the G x E interaction, in particular, when we are in the situation of identifying a single genotype which is ideal for various environments with different types of stress.

Only after having obtained all these information and having analysed them in a combined and/or separate manner for each type of environment, will it be possible to supply a concrete contribution to those who work daily in these difficult environments and to accelerate the provision of material which is truly tolerant to water stress in each environment. Finally, help must also come from molecular marker technology, because difficulties in identifying and conducting reliable drought-resistance screens can be overcome by improving the efficiency of selection for drought resistance via the use of molecular markers.

Key words: Sunflower, agronomic traits, breeding, drought tolerance, environment, plant adaptation

INTRODUCTION

During last 20 years, crops of sunflower have extended throughout the European Mediterranean countries due to its capacity to adapt to dry environments. Although a plant moderately tolerant of drought, production from this oil crop is strongly influenced by the presence of water stress which is found fairly regularly.

In fact, summer drought is a permanent feature in Mediterranean areas and may also periodically influence the economies of the countries adjoining of the true Mediterranean zone from the north.

The threat from the trends in the global climate render this property ever more important. At a scientific level there is a mass of work on the relationship between water supply and plant yield, but most deal with crops under irrigation. In contrast, useful knowledge concerning the improvement of the species to environments with trophic, especially water, limitations are still scarce and fragmentary. In our paper we have attempted to establish the state of the art of research into the strategies to adopt for improving drought resistance in sunflower, whilst trying to identify which of the many agronomic factors may be used to improve the efficiency of selection processes. We have chosen not to consider the importance of physiological parameters, for reasons of brevity, even though the latter have often been used both by ourselves and other researchers when faced with genetic variability in the genus *Helianthus* obtained with interspecific crosses

European agriculture in the 1990's

The increase in yield per unit surface area, which was the main objective of European agriculture in the 1970's has, during the course of the overproduction of some crops in the 1990's, been joined by other objectives such as the improvement of quality, stability of yield and the need for sustainable agriculture, by which we mean agriculture with compatible the environment.

The physiological processes have been divided into their components at a cropping level, and plant genetics have been worked on to obtain the ideal type of plant containing the best characteristics for a given environment. These were the elements considered in defining the "ideal crop", i.e., the result of the interaction between the ideal type and the agricultural techniques which are required for a genotype to attain its best expression in a given environment. In a marginal environment with a limited availability of production factors (water, fertilizers, ...), the research objectives for crop production and genetic improvement cannot be based on the maximum genetic uniformity and the use of the best production techniques, but must assist agricultural systems with low inputs, based on the exploitation of wide genetic variability with the aim of obtaining the highest efficiency of exploitation of the limited resources available, specific resistance to biotic and abiotic stresses and the stability of the yield (Monti, 1990).

Definition of drought environments

It is well-known that drought is the condition in which the water availability is reduced to the point where the plant is unable to absorb water sufficiently rapidly to compensate for transpiration (Osmanzai *et al.*, 1987). There are various types of drought which depend on the interaction of a series of factors including: precipitation, temperature, relative humidity, soil moisture, etc., with the plant genotype.

In characterizing a drought environment it is also important to identify the timing and severity of water stress in relation to crop phenology:

- 1) *Early stress*. In some cases the dry period may occur after sowing and young seedlings may suffer from water stress. Early-maturing cultivars may be affected severely by early season drought, whereas late-maturing cultivars may have sufficient time to recover from it.
- 2) *Mild, intermittent stress*. Short intermittent stress that can develop at any time during the crop cycle may cause large reduction in yield.
- 3) *Late stress*. This is typical of Mediterranean environments and the crop during the flowering-grain filling period is affected by drought.

Even if the water stress situations are not well defined, (as it is possible to have various combinations of the situations described above), the frequency of occurrence of these three types of water stress in the target regions should be determined as the first step in any drought-resistance research program. Comparison of grain yield in experiments which compare rainfed and irrigated conditions will provide information on the magnitude of the drought problem.

It should be mentioned that drought may also affect crop growth indirectly, through the incidence of other adverse conditions. Certain diseases, e.g., *Macrophomina phaseoli*, in sunflower develop under dry conditions and some cultivars appear to perform better with respect to others in some dry years. In these situations, the specific drought-resistance response is confounded by the presence of disease. Where disease occurs widely with drought, direct selection against the dis-

ease may be more appropriate than attempting to develop cultivars with drought resistance alone.

Plant adaptation mechanisms to drought

In field crop production, survival alone during a drought is not sufficient; the crop needs to produce a reasonable yield for subsistence requirements or for economic reasons. From an agronomic point of view, drought resistance refers to the capacity of cultivated plants to supply an economically acceptable product under limiting conditions of soil moisture (Qualset, 1979) In this sense Sojka *et al.* (1981) defined drought resistance as the capacity to minimize the loss in production in the absence of an optimum availability of water in the soil.

The four common adaptation mechanisms in crops are drought escape, dehydration avoidance, dehydration tolerance and drought recovery. Each mechanism may be the result of a number of traits (Levit, 1972).

Drought escape

The most effective method of minimizing the adverse effects of drought is for the crop to grow during the period of high rainfall and high soil water availability, i.e., to escape the dry period. Crop duration is important in determining grain yield because quick-maturing cultivars often escape a terminal stress while late-maturing cultivars may be affected by it. Timing of drought development in relation to phenology is also important for the determination of grain yield. It is well-known that the stage from first to post anthesis is most sensitive to water stress in sunflower. Thus it is likely that cultivars with different phenology will react differently to drought, depending on the timing of the stress. These results suggest that genotypes should be compared for drought resistance/susceptibility within the same phenology group, or at least genotypic variation in phenology should be corrected in some way before differences in drought resistance are estimated.

Dehydration avoidance

This is a mechanism for avoiding low plant water status during a drought period. Plants can maintain relatively high leaf water potential in several ways. One is to extract more water from the soil, while another is to use soil water slowly during the early stages of a drought period so that more is available later in the period. Plant water status is determined by the balance of water uptake through the root system and water demand by the shoot.

Thus it appears that one of the key research areas for drought resistance is to identify traits which lead to the maintenance of high leaf water potential during dry periods.

Dehydration tolerance

This is a mechanism by which plants maintain metabolism even at low leaf water potential. When stress develops during grain filling, dehydration tolerance may allow the plants to maintain metabolic activity for a few additional days and hence continue the translocation of previously produced assimilates to fill the grains. In sunflower, the redistribution of assimilates for grain filling could be important.

Drought recovery

This is an important mechanism when drought occurs early in crop development. Recovery of a genotype from drought is related to its ability to retain green leaves during that period. Leaf retention may be particularly important when stress develops around flower initiation, because lines with good leaf retention can supply more assimilate to the developing flowers during subsequent recovery.

Strategies for the genetic improvement of drought resistance

A) Traditional, with yield as the only selection criterium

In conventional breeding, the debate is between those who advocate selection in favorable environments, where genetic differences are maximized and environmental noise minimized, and those who believe that selection has to be done in the target environment or in conditions as near as possible to it. Blum (1979) clarified the existence of these two distinct possibilities for selection for drought-prone environments: selection for high production potential in optimum environments, considering that the genotypes with this characteristic may have a high yield even under stress conditions, due to their high residual yield and that, whenever the environmental conditions are favorable, these varieties will be ready to exploit their potential; otherwise, selection for high yields in the target environment may be conducted under drought conditions. In this case the genotypes obtained would certainly have some production advantages in that type of environment, but would not have the characteristic of production potential capable of exploiting favorable periods during the season.

The presence of the Genotypes by Environments (G x E) interaction, which affects the ranking of breeding lines in different environments, determines the preference for the second approach by the majority of geneticists and physiologists.

Hanson and Nelsen (1980) have established that conventional improvement for drought resistance has the following limiting factors:

- 1) production is under complex genetic control (being the result of many characteristics) with strong interactions with the environment;
- 2) adopting this parameter makes it difficult to use single plants as the unit of selection;

- 3) adaptation problems towards a given environment, such as susceptibility to a given disease, may eliminate genotypes with favorable components for drought resistance.

These limitations are in addition to the reduction of the values obtained from the estimates of the heritability of the yield determined in limiting environment which depresses genetic variability (Frey, 1964; Roseille and Hamblin, 1988), so that the adoption of this criterium alone means that selection becomes even more inefficient, and it is necessary to use very large populations to obtain appreciable progress from selection.

- B) *Indirect improvement of yield via the putative trait which considers the possibility of utilizing characteristics (agronomic, morphological, physiological, ...) other than yield, controlled by different genetic systems and which may be selected for independently (Richards, 1987).*

The above considerations suggest that the use of particular drought-resistance traits as selection criteria may improve the efficiency of breeding programs.

The major determinant of the scope for indirect improvement of yield via the putative trait is the heritability of the trait and genetic correlation between the trait and yield.

Information on the heritability of individual traits and their genetic correlations with yield would allow an objective assessment of the indirect response to selection for yield.

In summary, the work by Clarke (1987), Hanson and Nelsen (1980) indicate that for an indirect improvement of yield via the putative trait for drought resistance it is necessary to:

- 1) define the type of drought which occurs during the life cycle of the crop;
- 2) identify the quantifiable characteristics, both favorable and unfavorable; distinguish between the constitutional and adaptive characteristics; these latter express themselves as the gradual and continual response to specific stimuli;
- 3) determine the existence of a variation;
- 4) study the heritability of the characteristics considered and the genetic correlation with the production in drought conditions and in the phenological stage during which these characteristics express themselves;
- 5) study the responses to drought under controlled environment conditions and develop rapid and applicable methods for identifying these responses preferably in an earlier development stage than the production stage.

G x E interaction and selection for drought resistance

Genotype by environment (G x E) interactions are expressed as a change in the relative performance of genotypes in different environments. These interactions complicate selection of superior genotypes when they are largely relative to genotypic variation and particularly when they result in a change in the rank of geno-

types across environments. The incidence, size and nature of G x E interactions are commonly investigated by conducting multi-environment trials in which a sample of genotypes is evaluated at a number of sites over a number of years.

The problem becomes even more complex as numerous characters are inherited in a quantitative manner and they are all largely influenced by the environment; for this reason it is necessary to obtain as many information as possible on the genetic differences between varieties and populations and their responses to different environments, that is, the genotype-environment interaction (Cubero and Flores, 1994). These authors reported that the G x E interaction may partly be interpreted as a result of differential response to different environmental stresses (drought, salinity, etc.) and consequently the improvement in resistance would translate itself into an increase in stability. However, in general, only a small portion of the G x E interaction can be attributed to known environmental factors. The rest is composed of an unexplainable quantity in the statistical analyses of yield trials, generally known as experimental error.

Statistical models and methodology for the analysis and interpretation of such series of experiments have been widely discussed (Nyquist, 1991; Cooper *et al.*, 1993; Cooper and DeLacy, 1994). Such analyses allow an evaluation of the size of the G x E interaction variation relative to genotypic variation for the plant traits studied. Most of these statistical routines are highly related to the agronomic concept of stability, including the single and multivariant parametric methods, while non-parametric methods are less commonly used.

The most popular univariate methods are based on the regression coefficient of each genotype from the environmental mean, with the most well-known techniques being those proposed by Finlay and Wilkinson (1963), Eberhart and Rusell (1966) and Freeman (1973). Although these methods have been extensively employed, there are also numerous important papers which criticise their use. Cubero and Flores (1994) reported that these methods have a weak theoretical basis and they listed numerous defects, which may be summarized in the two points below:

- 1) there is no definition of the aspects of the environment that are important in discriminating between genotypes;
- 2) there is no understanding of the characters which contribute to the differences in yield adaptation expressed between genotypes.

More recent are the multivariate methods for the analysis of stability. These methods provide wide and useful information concerning the true response of the genotypes to the environments (Cubero and Flores, 1994). Two groups of multivariate techniques have been used to study the internal structure of the G x E interaction:

- 1) Order Techniques, such as Principal Component Analysis (Cubero and Fidres, 1994), Principal Coordinate Analysis (Westcott, 1986; Westcott, 1987), Factorial Analysis (Hill, 1974; Westcott, 1986) and AMMI Analysis (Mandel, 1971);

- 2) Classification Techniques, such as the Analysis of Groups by Fox and Rostelle (1982) and the analysis of Groups by Lin (1982).

AMMI analysis

AMMI (Additive Main Effects and Multiplicative Interaction) analysis was proposed by Mandel (1971) and consists of a two dimensional matrix of the G x E interaction, using a multiplicative method. AMMI studies the main additive effects of genotypes and environments by analysis of variance (ANOVA) and describes the non-additive portion of the variation, that is the G x E interaction, with an analysis of the principal components. This method has three main objectives (Cubero and Flores, 1994):

- 1) diagnosis – it diagnoses the possibility of studying sub-models which are representative of the entire dataset in the trial;
- 2) clarification of the G x E interaction – it provides schemes and behaviour modes for the genotypes and environments combined;
- 3) improvement of the precision of yield estimates.

Gauch and Zobel (1990) have demonstrated the existence of three main practical advantages:

- 1) it allows an improved identification and selection of the superior genotypes;
- 2) it allows more flexible and efficient experimental designs;
- 3) it is only slightly sensitive to missing data; in fact, for each treatment there are direct data (those from the treatment) and indirect data (all the other data from the trial).

Gauch (1988) and Gauch and Zobel (1988) have indicated the possibility of using the AMMI model with a predictive approach, in addition to its "posdittivo". From the "posdittivo" point of view the data are used to construct a model that explains the data and compares the expected values with the starting values. With a predictive approach, the data are divided into two parts – those which are required to operate the model, or rather the data analysed by AMMI, and those used for the validity testing.

Zerbi *et al.* (1997) believe that in variety trials the model AMMI has a higher predictive accuracy than the standard methods. The efficiency of AMMI increases with the dimensions of the variety trial and with the error of the trial itself. The increase in accuracy of the AMMI method over traditional ANOVA has been estimated to be 4.3 fold (Crossa *et al.*, 1990). It is thus possible to use a number of replicates 4.3 times smaller with the same degree of precision, or to increase the precision 4.3 times with the same number of replicates.

Cubero and Flores (1994) showed that estimating the yield of the genotypes with the maximum accuracy was an important aspect of genetic improvement trials performed in different environments. They warned that an obstacle to these estimates is often the "noise" and errors in the field data. They also explained that in practice the noise in an AMMI analysis can be quantified with the Sum of the Resid-

ual Squares, after having adjusted the best prediction model, and the error can be estimated with the differences between the individual experimental units (repetitions) within a given treatment (combinations of G x E).

AMMI has found an ideal application in the networks of variety comparison trials (Cossa *et al.*, 1991; Gauch, 1992; Cornelius, 1993), in the study of adaptability, the interaction G x E and the stability of lucerne (Annicchiarico, 1992), maize (Annicchiarico *et al.*, 1995) and sunflower (Alza, 1995) and in the choice of the location for the variety trials (Saindon and Schaalje, 1993) and the identification of the environments suitable for the cultivation and selection of wheat (Annicchiarico and Perenzin, 1994).

Appropriate traits for various drought environments

This section so far has shown that a number of traits could possibly assist the development of drought-resistant cultivars. It should be pointed out, however, that in most cases the usefulness of individual traits in contributing to greater yield has not been demonstrated. It is therefore essential that the value of traits be established before they are used as selection criteria. Grain yield is a result of many interacting processes, and thus it is not surprising that there is a large G x E interaction which makes it difficult to explain the contribution and demonstrate the value of individual traits unless the growth environment is fully defined.

For example, retention of flower fertility appears important in maintaining high seed yield under flowering-stage drought. However, this does not necessarily mean that lines with high flower fertility have special mechanisms in the flower; rather, they may have higher leaf water potential as a result of the effect of a primary trait, for example a deep root system. Thus, gene(s) responsible for the high flower fertility may be those associated with the root system. Screening for high flower fertility may be successful to some extent, but this may relate to the stability of maintenance of high leaf water potential under different types of drought. Since variation for leaf water potential is associated with expression of many traits, it is critical to examine whether the expression is the result of variation for leaf water potential, or if the trait is the reason for the water potential variation.

The mechanisms for tolerance to abiotic stresses in the plant are not completely understood, despite years of research in this sector. While it is fairly clear that there are several integrated mechanisms which control the tolerance to abiotic stress factors, and there are good indications concerning phenological, morphological and physiological characteristics which are suitable for adaptation to drought (Feres *et al.*, 1986; Baldini *et al.*, 1992), it is still not clear how these characteristics are integrated and correlated to constitute specific mechanisms for adaptation to drought, at a tissue or organ level, and to determine the seed yield.

A number of agronomic traits in sunflower are now considered.

1. Phenology

Studies of heritability in sunflower for the number of days to flowering give relatively high values, 90% in the widest sense (Shabana, 1974), 66% in the narrow sense (Baez *et al.*, 1988), 98% (Dominguez, 1989) and 90% (Alza, 1995). The ACG and ACS' values suggest that the additive effects are more important than the non-additive ones (Putt, 1966). In general, the number of days to flowering is correlated with the number of days to physiological maturity (Fick, 1978). Baez *et al.* (1988) found significant correlation coefficients (0.86 and 0.91) between the number of days to flowering in hybrids and their parents, and this is in agreement with the high values of heritability (43%) of the character 'number of days in flower', that is the number of days between the beginning of flowering and physiological maturity.

When evaluating the usefulness of traits to increase grain yield, it is important to consider phenological development which has an overriding effect on grain yield under water-limiting conditions. Comparison of lines with different phenology is difficult, as stated earlier. When lines are compared at different sowing dates or locations, there is likely to be a large G x E interaction for days to flowering because of differential genotypic responses to temperature. This interaction complicates comparisons of genotypic response to water stress in different experiments.

Table 1: Heritability in narrow sense of yield and some agronomic characters in sunflower under drought conditions

Yield	Sowing-flowering period	Head diameter	Stem diameter	Seed weight	Seed number	% of sterile head area	LAI	Total biomass	H	Seed oil %	S index	Authors and locations
0.38					0.45				0.46			Baldini <i>et al.</i> , (1992); Pisa, 1990
0.24					0.34				0.32			Baldini <i>et al.</i> , (1992); Pisa, 1991
0.57	0.95	0.72	0.67	0.70	0.56	0		0.64	0.49	0.29	0.39	Alza and Fer-Mart. (1997); Cordoba, 1987
0.07		0.24	0.54	0.85	0.56	0.67		0.55	0.55	0.52		Alza and Fer-Mart. (1997); Sevilla, 1987
0.44	0.91	0.45	0.60	0.88	0.52	0.73	0.42	0.72	0.68	0.81	0.58	Alza and Fer-Mart. (1997); Cordoba, 1988
0.24										0.56	0.32	Alza and Fer-Mart. (1997); Sevilla, 1992
0.27	0.94			0.90	0.44		-			0.35	0.41	Gomez-S. (1998), means across 10 locations

- : value lower than 0

Heritability estimates by Alza and Fernandez-Martinez (1997) and Gomez-Sanchez (1998) for days to flowering were very high and consistent across environ-

ments under drought (0.91-0.95) (Table 1). The same authors found positive values of genetic correlations with yield in the same environments under rainfed conditions, confirming that a selection to lengthen or shorten the sowing-flowering period has concrete possibilities of success even under stress conditions as shown by the data reported above (Table 2).

Table 2: Genetic correlations among yield and some agronomic characters under drought conditions

Sowing-flowering period	Head diameter	Stem diameter	Seed weight	Seed number	% of sterile head area	LAI	Total biomass	HI	Seed oil %	S index	Authors and locations
0.44-0.59	0.49-0.96	0.79	0.57-0.76	0.49-0.70	-0.45/-0.55	0.51	0.76-0.92	-0.16-0.45		-0.14/-0.4	Alza and Fer-Mart. (1997), data as range of the locations
-0.12			0.68	-0.39		0.86			0.66	-0.44	Gomez-S. (1998), as means across 10 environments

This strategy will lead to concrete advantages only if the period of stress in the crop environment is predictable and starts in a late phase of vegetative development (in flowering); only in this case can quick-maturing cultivars escape drought stress (drought escape mechanism) while late-maturing cultivars may still be affected by it.

In our experiments (Baldini and Vannozzi, 1998) genotype differences in flowering time did not seem to influence the response to a terminal drought. In contrast, Gimenez and Fereres (1986) found that long-season genotypes outyield short-season cultivars under rain-fed conditions in a Mediterranean environment (south-western Spain) with a late drought stress period. However, the explanation of the above result is the positive relationship between the depth of root in the long-season genotypes and the particular environment, where sufficient water was stored in the soil profile, down at 270 cm, but was not available to short-season genotypes.

2. Root system

Roots play a major role in maintaining the water supply to plant tissues. Variation in root growth between and within species is recognized to be a characteristic determining the differences in drought resistance. Only a limited quantity of research on the genetic variability of root characteristics has been performed with crop species, especially sunflower, probably because the determination of root thickness, root dry weight and root length density in the field is time consuming, and quicker methods which could be used in screening in breeding programs for

ideal root systems are lacking. Genotypic variation in root systems, soil water extraction and its implications for drought resistance in sunflower was obtained by Gimenez and Fereres (1986). They found that short-season cultivars extracted all the available soil water down to 120 cm and extraction became negligible at 150-180 cm. In contrast, long-season genotypes fully depleted the soil reserves down to 180-210 cm, and some genotypes even exhibited substantial extraction at 270 cm. This suggested that long season cultivars had deeper root systems and generated a larger soil water potential gradient and consequently a greater upward flux of water from the deep and wet soil layer. The genotype differences in root depth were important for selection under rainfed conditions especially in Mediterranean climate environments where deep stored water may be present at sowing. In contrast, negligible benefit can be expected by increasing root depth in some environments in central Argentina, where intermittent drought stress is present (Sadras and Hall, 1989; Sadras *et al.*, 1989). In this case, genotypes with a high root density in the 0-0.2 m soil layer could benefit more from intermittent rain. The difference in the response of crops in these two contrasting environments demonstrates the importance of local patterns of water availability in the determination of traits contributing to drought tolerance.

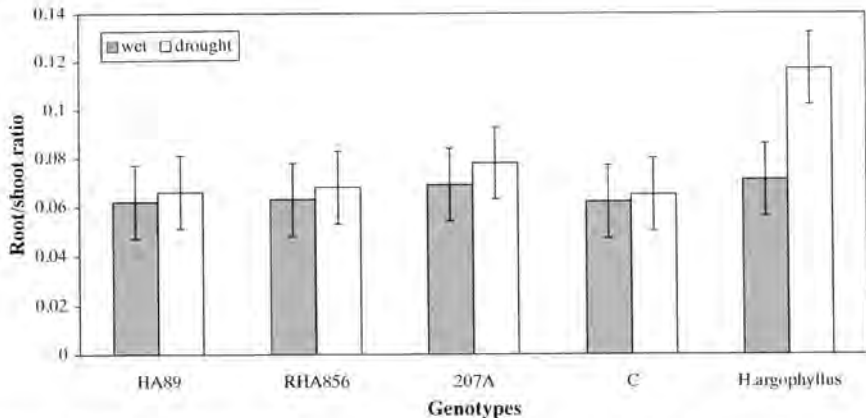


Figure 1: Genotype \times treatment interaction for root/shoot ratio under a partially conditioned environment. Bars represent the standard deviation of the mean ($n=3$), (data from Baldini *et al.*, 1993)

Differences in root/shoot ratio between genotypes were observed in our experiment, probably due to differences in drought treatment and genetic characteristics. In fact, in a conditioned experiment, the root/shoot ratio of a wild species (*Helianthus argophyllus* T & G) increased under a late drought treatment (Figure 1), while the same character, in the other cultivated genotypes, was unchanged (Baldini *et al.*, 1993). In another experiment carried out in a partially conditioned environment at Udine University, the ratio decreased and was lower in the most resistant inbred

lines (from the above wild population) than the other cultivated genotypes (Figure 2); (Baldini and Vannozzi, 1998).

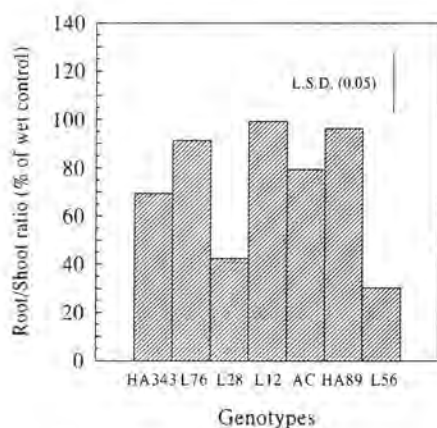


Figure 2: Root/shoot ratio under drought conditions, expressed as % of the wet control. The vertical bars represent the L.S.D. value at $P < 0.05$, (Baldini and Vannozzi, 1998).

3. Plant height

In many studies a positive and significant correlation has been observed between this character and the biomass, the number of leaves, the diameter of the head, the leaf area index and the achene yield, under both irrigated and drought conditions. Numerous authors have published results from studies of the heritability of this character, which vary according to the method adopted. Pathak (1970) estimated heritability in the widest sense with a value of 20%, Shabaria (1974) 90%, Fick (1978) obtained values between 41 and 85%, in the wide sense and from 20.4 to 37.5% in the narrow sense. In other studies the estimate of heritability, in relation to the female and male lines, was 92 and 84% respectively (Škorić, 1974). Alza (1995) found values between 57 and 88%.

These studies suggest that the non-additive genetic effects are relatively more important than the additive effects in controlling the characteristic. In a study of the suitability for combination, Tyagi (1988) demonstrated that both the additive and non-additive genetic effects were equally important in determining the height of the plant and also reported highly significant differences for ACG and ACS. Alza (1995) observed that the ACG from the maternal stock was more important than the ACS.

4. Stem diameter

The narrow heritability of the stem diameter calculated by Alza and Fernandez-Martinez (1997) is elevated, higher than yield value and consistent across environments (Table 1). The genetic correlation with yield is equally elevated (0.79) (Table 2).

5. LAI and LAD

The Leaf Area Index is a characteristic which is often correlated with the achene yield (Škorić, 1974; Shabana 1974; Fereres *et al.*, 1986; Alza, 1995). In sunflower, the maximum interception of light is obtained when the LAI reaches values of 2.5 to 3.0, and the highest achene yield occurs when these values are found in plants at 50% flowering (Merrien, 1992). In the inheritance of this characteristic, the non-additive genetic component is more important than the additive component, so there is a high heterotic effect (Marinković and Škorić, 1985). Even more important than the LAI is the duration of the leaf area (LAD), which, especially after flowering, is a characteristic which is positively correlated with the achene yield (Merrien *et al.*, 1982; Hall *et al.*, 1985; Gimenez and Fereres, 1986). The LAD is particularly influenced by the soil water availability. When drought conditions are encountered during the early development phases of the plant, the development of the leaf area is modest and the number of leaves reduced. If there are other water deficit periods, during flowering, the senescence processes occur early (Merrien, 1992). Genotypes with high LAI values and the capacity to maintain their LAI during the seed filling process are those with characteristics which are clearly important for tolerance to drought (Miller, 1992).

The inheritance of these characters is not available in sunflower under drought conditions. The exceptions are the experiments carried out by Alza and Fernandez-Martinez (1997), obtained in only one environment (Cordoba, 1988), where they found a value of 0.42. Conversely, Gomez-Sanchez (1998) found a very low value, estimated across 10 environments in rainfed conditions. Both of the above values were lower than the heritability in the narrow sense obtained for yield (Table 1). The genetic correlation between LAI and yield, calculated by the same authors, was medium-low (Table 2).

6. Total biomass

The estimate of narrow sense heritability was reported to be positive and higher than that of yield in the three experiments under drought of Alza and Fernandez-Martinez (1987). At the same time, the genetic correlation between these two characters was positive and elevated (0.76 - 0.92) (Table 1 and 2).

These values agree with our results obtained in 1994 and 1995 at Udine University, where the correlation between seed yield and biomass accumulation under drought was 0.88 (Gomez-Sanchez *et al.*, 1998). The relationship between biomass yield and drought tolerance also appeared in our experiment carried out in a partially conditioned environment (Figure 3), where the drought treatment significantly reduced stover dry weight per plant compared with the well-watered treatment, but

L76 and L28 (the most resistant genotypes) exhibited the smallest reductions (13.6 and 20.5%, respectively) (Baldini and Vannozzi, 1998).

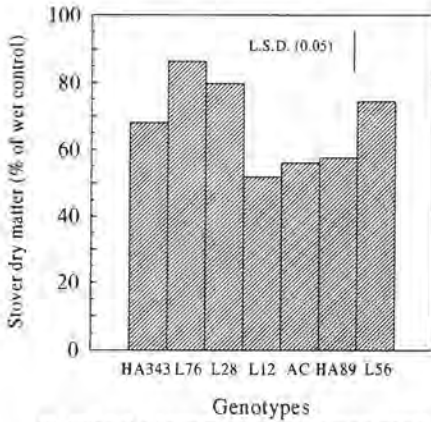


Figure 3: Stover (leaves + stem + receptacle) dry weight under drought conditions, expressed as % of the wet control. The vertical bars represent the L.S.D. value at $P < 0.05$, (Baldini and Vannozzi, 1998).

7. Head diameter and inner sterile area of the head

Head diameter and inner sterile area of the head showed heritabilities higher than the yield in the rainfed conditions in all locations tested by Alza and Fernandez-Martínez (1997). The same authors found a positive and high genetic correlation between head diameter and yield (0.49/0.96 as the range across locations) and a negative correlation (-0.45/-0.55) between the inner sterile area of the head and yield. From our experience, inner sterile area of the head increased under drought conditions in most susceptible genotypes up to 63.7%, with respect to their controls; in contrast, the drought conditions did not significantly affect the sterile area of the head in the more tolerant genotypes.

8. Seed weight and seed number per head

The seed weight is a characteristic which is often strongly influenced by water availability (Feres *et al.*, 1986; Gimenez and Feres, 1986). For this reason, thousand seed weight is a characteristic which has been widely considered in genetic improvement for drought tolerance. The type of gene action, in the heritability of this characteristic, depends on the genotypes evaluated. Piquemal (1968) found that this component of yield has the highest heritability. Pathak (1974) and Shabana (1974) estimated wide sense heritability values of 30 and 66% respectively. Putt (1966) found that the importance of the components of ACG and ACS was equal for both and suggested that the additive and non-additive effects are equally important in the genetic control of seed weight. In contrast, Marinković and Škorić (1985) found that the superdominance, or the dominance of the best parent, is expressed in the F_1 . Kovačik and Škaloud (1977) found a non-additive component many times greater than the additive component for this characteristic. Keste-

loot *et al.* (1985), in a diallel cross, found significant differences for ACG and ACS, a heritability of 60% and a correlation of 0.73 with achene yield.

The number of seeds per head is one of the most important components of the achene yield (Vranceanu, 1970; Shabana, 1974; Kesteloot *et al.*, 1985). The factors capable of inducing variations in the number of seeds per head are: the potential number of flowers, which is determined during the vegetative period of the plant and principally by the development of the leaf area (Picq, 1986), the dry matter produced and the absorption of nitrogen (Steer and Hocking, 1983), at the end of the vegetative period. Seed abortion can be observed under drought conditions during the flowering period. In cases of water stress, the plants with a reduced leaf area, caused by early senescence, will have a reduction in the number of seeds per head (Merrien, 1992). Rao and Singh (1977) postulated that the principal component of the genetic variance of this characteristic was non-additive. Kesteloot *et al.* (1985) found a heritability of 75% in the F_1 generation of a diallel and significant differences in the ACG and ACS. Tyagi, in contrast (1988), found significant differences only for ACG.

Seed weight and seed number per head are considered together because they are strictly dependent, as yield components, on water deficit; in fact their adjustment follows a compensation mechanism well known in sunflower (Merrien, 1986).

Estimates of narrow sense heritability were very high (more than 70%) in all environments of the trials carried out by Alza and Fernandez-Martinez (1997) and Gomez-Sanchez (1998), confirming that additive gene action predominantly influenced the expression of this trait under drought (Table 1). The genetic correlation with seed yield under drought was consequently high and positive in the same experiments (range between 0.57 and 0.76) (Table 2).

The narrow heritability of seed number calculated by the above authors and by Baldini *et al.* (1992) range between 0.34 and 0.56 and it was lower than the values obtained for seed weight, but higher in all environments, with the exception of Cordoba 1987, than the heritability of seed yield (Table 1). The genetic correlation with seed yield under drought was positive in the same experiments (range 0.49 and 0.70) (Table 2).

Table 3: Regression analysis of the ratio of full seed number (FSd/FSw) and of the ratio of seed weight (SWd/SWw) against the susceptibility index (S); a and b are coefficient of the equation, r is the correlation analysis and n is the number of data

Character	a	b	r	n
FSd/FSw	164.7	-92.9	-0.75**	28
SWd/SWw	53.5	19.2	0.25 n.s.	28

** : $P < 0.01$; n.s.: not significant

Baldini and Vannozzi (1998) separated the effects of filled seed number and seed weight on seed yield under drought by correlating S (susceptibility index) with the ratio of the number of filled seeds per head (FSd/FSw) and the ratio of seed weight (SWd/SWw) between the dryland and the irrigated treatments. The results

indicated a negative correlation between FSd/FSw and S (-0.75**) and no correlation between SWd/SWw and S index (Table 3). Thus, the genotype differences in S must be mostly attributed to adjustments in the number of filled seeds per head under dry conditions and not to individual seed weight, as already reported by Ferreres *et al.* (1986). The above results were confirmed by another trial carried out by Baldini and Vannozzi (1998) in a partially conditioned environment in Italy, where the seed number and fertility ratio were unaffected by drought in the tolerant genotypes (Figures 4 and 5), while the seed weight drastically decreased in the same genotypes (Figure 6).

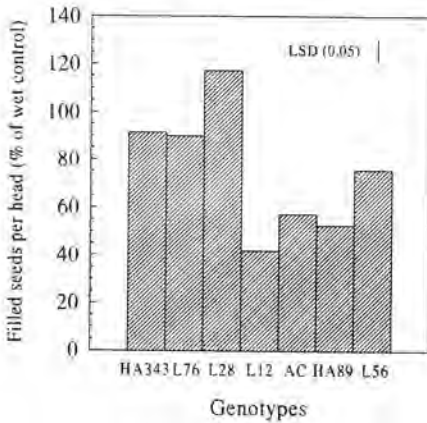


Figure 4: Filled-seeds number per head, expressed as % of the wet control. The vertical bars represent the L.S.D. value at $P < 0.05$, (Baldini and Vannozzi, 1998).

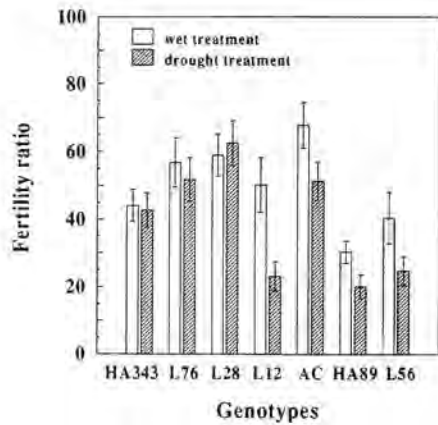


Figure 5: Fertility ratio (filled/seeds/flowers number per head) under wet and drought conditions. The vertical bars represent the L.S.D. value at $P < 0.05$, (Baldini and Vannozzi, 1998).

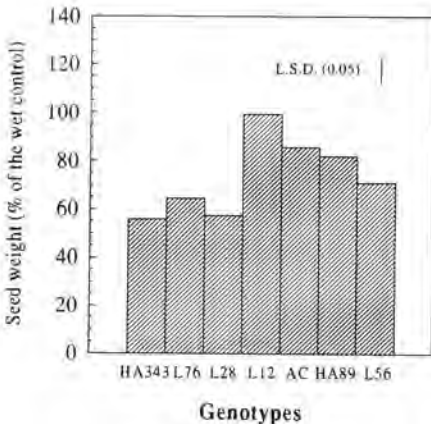


Figure 6: 100-seed weight under drought conditions, expressed as % of the wet control. The vertical bars represent the L.S.D. value at $P < 0.05$, (Baldini and Vannozzi, 1998).

9. Seed oil content

The oil content in sunflower achenes mainly depends on the proportions of husk and kernel (Gundaev, 1971; Fick, 1978), the water stress and high temperatures (Muriel and Downes, 1974; Fereres *et al.*, 1986). Fernandez-Martinez and Domínguez-Gimenez (1985), in a study of the variability of the characteristics of sunflower seeds, found values between 23 and 56% of oil in the achenes. According to Alexander (1963), the achene oil content is subject to a complex polygenic control, with a strong additive genetic effect, which explains the success obtained in the selection of this characteristic by modified recurrent selection. Putt (1966) also found a higher ACG value than the ACS, and this indicates the existence of a strong additive component, in agreement with the results obtained by Bedov (1985) and Refoyo *et al.* (1985).

Fick (1975) found that the narrow sense heritability of oil content varied from 52 and 61%. Miller *et al.* (1982) found that 50% of the variation in achene oil content in sunflower hybrids was due to variability in the female line, and this fact implies a high heritability. Fernandez-Martinez *et al.* (1979), in a cross between a cultivated line with a high oil content and a line of wild sunflowers with low oil levels, found dominance for the low contents in the F_1 generation. Areco *et al.* (1985) also observed a tendency for the F_1 to have lower achene oil contents than the mean of the parent stock. Notwithstanding these results, in previous studies Fick (1975) observed that the F_1 had a higher value than the average of the parents, and this fact is in favour of the dominance of the characteristic "high oil content".

Heritability in the narrow sense for oil content under drought, as reported by Alza and Fernandez-Martinez (1997), with the exception of Cordoba 97, and Gomez-Sanchez (1998) is elevated and higher than that of yield (Table 1). The genetic correlation estimated by Gomez-Sanchez (1998) across 10 environments under rainfed condition was high (0.66) (Table 2). There is very little information of the use of this characteristic for drought tolerance and further genetic studies in drought-prone environments must be performed.

10. Harvest index

The heritability in the narrow sense estimated for HI is higher than that of yield in each environment under drought conditions considered in Table 1, with the exception of Cordoba 1987. The genetic correlation reported by Alza and Fernandez-Martinez (1997) (Table 2) among the rainfed yield and HI varied noticeably across years, but when long- and short-cycle hybrids were considered independently, these correlations were high and positive for both hybrids in all environments. The lack of consistency between environments agrees with the results obtained by Turner and Rawson (1982) and also with the results obtained by Fereres *et al.*, (1986) and by Gomez-Sanchez *et al.* (1998), when they included in the correlations the genotypes with different season lengths. In contrast, when the correlations were restricted to genotypes of the same length of season, the yield under drought was

directly related to the maintenance of harvest index. This fact was probably due to the high interaction between duration of the crop cycle and environment.

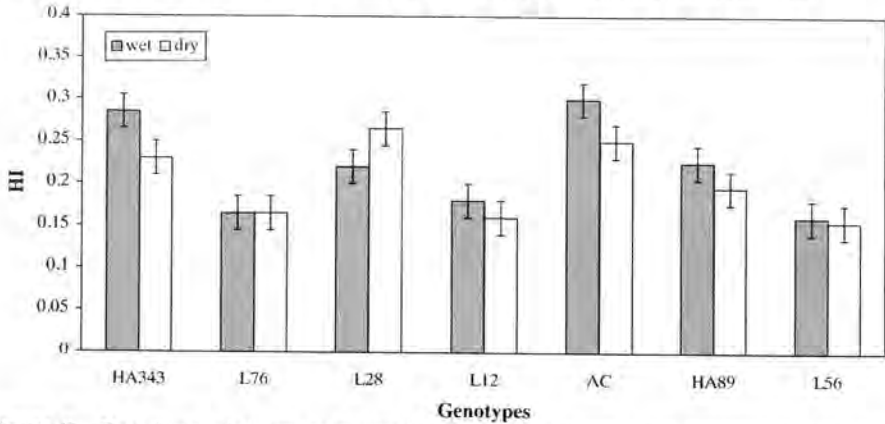


Figure 7: Genotype x treatment interaction, as means across two experiments, for harvest index (HI), (Udine, 1996-1997).

Our results in partially conditioned environments indicate that harvest index was substantially unaffected or reduced by drought in all genotypes, but significantly increased in L28, from 0.20 to 0.25 under drought (Figure 7). This result confirmed that plants which are tolerant to drought, such as L28, have a higher capability than others to translocate the late assimilates from the vegetative tissues to the filling seed.

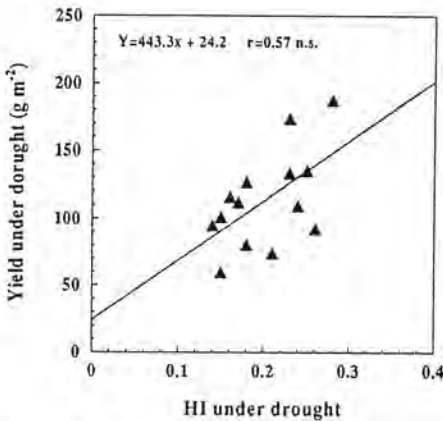


Figure 8: Relationship, across two trials, between seed yield and HI under drought conditions including the semi-dwarf line AC, n.s.: not significant

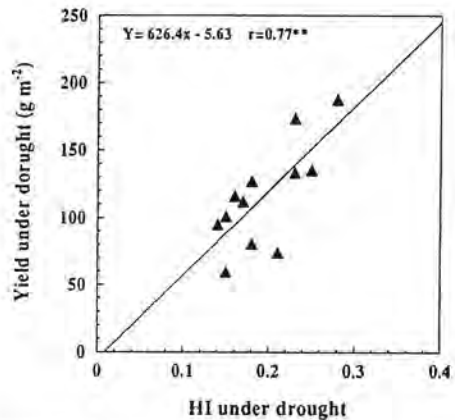


Figure 9: Relationship, across two trials, between seed yield and HI under drought conditions excluding the semi-dwarf line AC, **: significant for $P < 0.01$ probability level

The association between HI and seed yield was not observed when the AC genotype, characterized by a reduced height (semi-dwarf type), was included in the analysis (Figure 8); on the contrary, when the same genotype was excluded from the analysis, a significant and positive correlation ($r=0.77^{**}$) between HI and seed yield in drought conditions was found (Figure 9), confirming that the greater susceptibility of some genotypes to drought could be due to their low HI values (Baldini and Vannozzi, 1998).

11. Seed yield and susceptibility index (S)

Fisher and Maurer (1978) proposed the drought susceptibility index "S" calculated from the formula $1-(SYd/SYp)/D$, where SYd is the production under drought conditions, SYp is the production potential under irrigated conditions for each genotype, and $D=1-Xd/Xp$, that is the mean yield reduction under drought conditions for the entire trial, where Xd is the mean yield of all genotypes under drought conditions and Xp the mean yield of all genotypes under irrigated conditions. In these terms, very low values of drought susceptibility distinguish genotypes having greater resistance to drought.

Fisher and Wood (1979) demonstrated that drought susceptibility "S" was positively correlated with the potential yield and various characteristics under optimal growing condition for wheat, and the same has been demonstrated for maize (Fisher *et al.*, 1984). This relationship suggests that the improvement of the resistance to drought can only be obtained at the expense of potential productivity.

Today, in many works under drought conditions, of the numerous agronomic traits used to quantify drought resistance, the susceptibility index (S index) can be considered to be one of the most frequently used (Fischer and Maurer, 1978). It was calculated to distinguish and separate the effects of yield potential and drought susceptibility from yield under drought for each genotype, in order to explain part of the specific genetic effects as part of the total variation under drought. This character shows a heritability in the narrow sense which is slightly higher than that of yield under drought, with the exception of Cordoba 1987, as reported in Table 1 (Alza and Fernandez-Martinez, 1997; Gomez-Sanchez, 1998). Yield under drought and S are genetically correlated as shown in Table 2.

In our works, S index correctly identifies drought tolerant and susceptible genotypes across years and environments as reported in Figure 10; nevertheless, the seed yield needs to discriminate lines with similar S but differences in yield potential (Figure 11). The negative correlation between S and seed under drought conditions is reported in Figure 12 and in many other papers of ours (Baldini *et al.*, 1992; Gomez-Sanchez *et al.*, 1998; Baldini and Vannozzi 1988). Moreover, our results (Gomez-Sanchez *et al.*, 1998) reported an absence of correlation between S and yield potential (Figure 13) as already observed by Fereres *et al.* (1986) and Baldini *et al.* (1991) in similar experiments with sunflower hybrids.

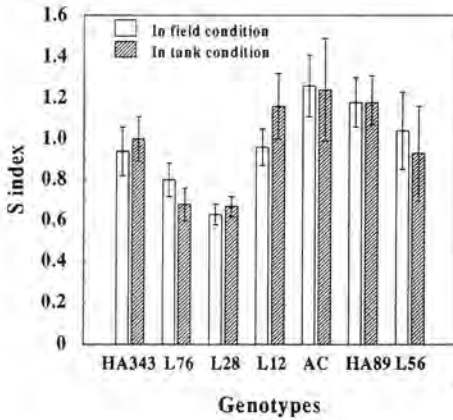


Figure 10: Drought susceptibility index (S) of sunflower inbred lines in tanks and field conditions. Vertical bars represent the standard deviation of the mean (n=3).

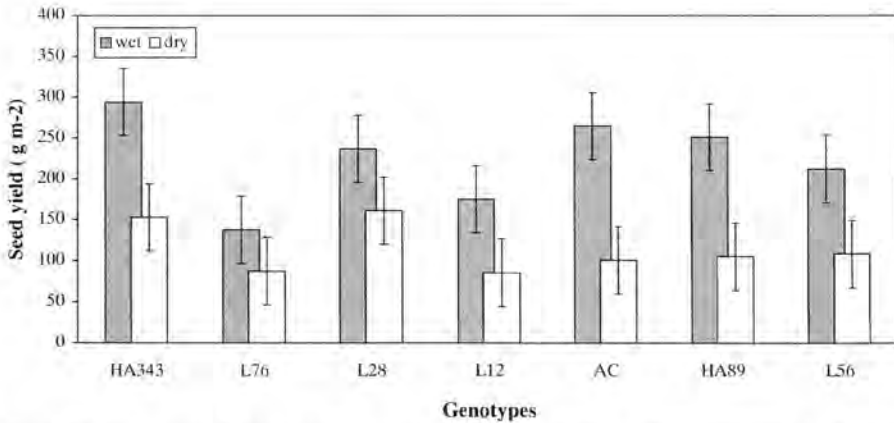


Figure 11: Genotype x treatment interaction, as means across two experiments, for seed yield, (Udine, 1996-1997).

These results indicate the concrete possibility of obtaining drought resistance and high yield potential in the same genotype and that the selection for high yield potential in favorable areas should be an efficient selection criterion to identify higher yielding materials for drought stress condition. The latter assumption was supported by the results obtained by Alza and Fernandez-Martinez (1997) and by Gomez-Sanchez (1998), who found the yield potential under well-watered conditions and yield under drought conditions were significantly and positively correlated across several environments and years in Spain and Italy.

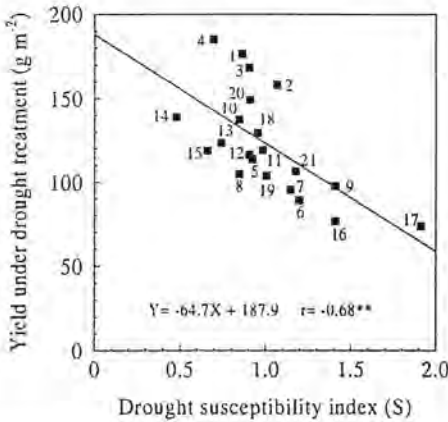


Figure 12: Relationship between *S* and seed yield under drought conditions. Number correspond to lines as in Table 1. **, significant for $P < 0.01$ probability level, (Gomez-Sanchez et al., 1998).

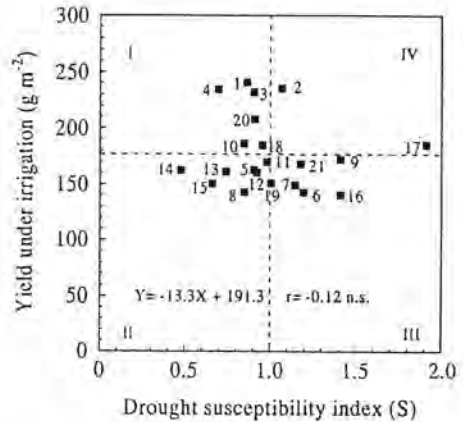


Figure 13: Relationship between *S* and seed yield under wet conditions. Dotted lines represent the averages of *S* and seed yield across years and genotypes. Number correspond to lines as in Table 1. n.s.: non-significant, (Gomez-Sanchez et al., 1998).

CONCLUSIONS

In the establishment of a genetic improvement program aimed at improving the resistance to water stress, the following points must be included :

- 1) define the types of drought environment which are encountered in the target environment for each plant breeding program, because different types of drought may require different approaches;
- 2) describe plant "ideotypes" once the target environment is accurately defined;
- 3) determine which traits are to be considered to assist the development of drought-resistant cultivars.

Before choosing the criteria to adopt in the choice of characteristics, it should be remembered that the identification of a single agronomic characteristic capable of reducing the susceptibility to drought is not at all easy because these characteristics often compete together to determine the production of seeds (so that they are not independent) and often their expression depends on physiological responses to the environment under examination, which is a consideration which we have not included in this paper, but which a plant breeder must be capable of recognizing and evaluating.

Table 4 lists suggested traits for enhancing the drought resistance of sunflower under various cultural conditions and types of water stress by our and other colleagues' data.

- 1) Given the particularly difficult conditions and unusual nature of drought-prone environments, accuracy is required in the identification of the selection method and the conduction of the experiment, in an attempt to steer the choice (identification of better progeny) towards data with a high number of replicates and not just single values.
- 2) Analysis of data which allow the interpretation of the G x E interaction. In particular, when we are in the situation of identifying a single genotype which is ideal for various environments with different types of stress and where, presumably, the G x E interaction will be high, it is important to select for the **stability** of the genotypes. Even when operating in a single environment, the G x E interaction and the stability, in this case **over time** and not in space, must be evaluated because different years will correspond to different climate trends. One of the most frequently used and promising methods is AMMI.

In conclusion, it should be stressed that today there is a general lack of drought related genetic characteristics for the various characteristics in situations of limited water availability.

Only after having obtained all these information and having analysed them in a combined and/or separate manner for each type of environment, will it be possible to supply a concrete contribution to those who work daily in these difficult environments and to accelerate the provision of material which is truly tolerant to water stress in each environment. Finally, help must also come from molecular marker technology, because difficulties in identifying and conducting reliable drought-resistance screens can be overcome by improving the efficiency of selection for drought resistance via the use of molecular markers.

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PROPIEDADES AGRONOMAS UTILES EN LA SELECCION DEL GIRASOL RELATIVA A LA RESISTENCIA A LA SEQUIA

RESUMEN

Durante los ultimos 20 años, el girasol se extendia en los paises en desarrollo a causa de su capacidad de adaptarse a las condiciones de sequia. Bien que sea una planta que tolera mediamente la sequia, el estres acuatico, que aparece casi regularmente, influye fuertemente sobre la produccion de esta cultura oleaginosa.

Efectivamente, la sequia es un fenomeno constante en muchos paises en desarrollo, y de tiempo en tiempo influye sobre las economias de Europa y EUA.

Las amenazas provocadas por los trends climaticos hacen este fenomeno aun mas importante.

En el campo cientifico, hay muchos estudios sobre la relacion entre la disponibilidad de agua y el rendimiento de plantas, pero la mayoria de esos estudios se refiere a las plantas cultivadas en las condiciones de irrigacion. Por el contrario, los conocimientos utiles sobre la adaptacion de esta cultura a las condiciones con las limitaciones tropicas, particularmente al respecto de la disponibilidad de agua, son poco numerosos y fragmentarios. En este estudio hemos probado a constatar el estado de cosas al respecto de la investigacion de estrategias a aplicar al mejoramiento de la resistencia a la sequia en el girasol, y al mismo tiempo de identificar cuales de muchas propiedades agronomas y parametros fisiologicos pueden utilizarse para el mejoramiento de eficiencia del proceso selectivo.

Elaborando el programa genetico destinado si mejoramiento de la resistencia al estres acuatico, debemos tener en cuenta las cosas siguientes:

- 1) Definicion del tipo de medio seco dominante en la region respectiva, particularmente para cada programa de seleccion, porque diversos tipos de sequia pueden exigir diversos accesos a su solucion.
- 2) Definicion de ideotipo vegetal cuando se define la region respectiva.
- 3) Determinacion de esas propiedades las cuales, creemos, puedan ayudar en la creacion de variedades resistentes a la sequia.
- 4) En caso de las condiciones excepcionalmente dificiles y de la natura insolita de la region expuesta a la sequia, es necesario definir precisamente el metodo de seleccion y la realizacion de experimentos para orientar la eleccion (identificacion de mejores descendencias) a los datos con mas grande numero de repeticiones en lugar de valores singulares.
- 5) Analisis de los datos que facilitan la interpretacion de la interaccion genotipo x medio ambiente, particularmente cuando encontramos la situacion de identificar un genotipo que sea ideal para las areas con diversos tipos de estres acuatico.

Solo despues de haber obtenido todos estos datos para cada tipo de region y de haber analizado los mismos combinados y cada uno, sera posible de hacer una contribucion concreta a aquellos que trabajan todos los dias en tales terrenos inhospitalarios y de acelerar el aprovisionamiento de material que tolera efectivamente el estres acuatico en todos medios. Finalmente, el ayuda tiene que llegar tambien de la tecnologia de marcadores moleculares, dado que las dificultades en la identificacion y la realizacion de testes ciertos de la resistencia a la sequia pueden ser superados por el mejoramiento de eficiencia de la seleccion relativa a la resistencia a la sequia por la utilizacion de marcadores moleculares.

CARACTÉRISTIQUES AGRONOMIQUES UTILES DANS LA SÉLECTION DU TOURNESOL POU SA RÉSISTANCE À LA SÉCHERESSE

RÉSUMÉ

Pendant les vingt dernières années, la culture du tournesol s'est étendue dans les pays en voie de développement en raison de sa capacité à s'adapter à des milieux secs. Quoique cette plante tolère modérément la sécheresse, sa production est fortement influencée par le stress dû à la carence d'eau qui est assez fréquent.

En fait, la sécheresse est un phénomène constant dans les pays en voie de développement et elle a aussi une influence périodique sur l'économie de l'Europe et celle des États-Unis.

Les menaces provenant des tendances climatiques actuelles accentuent l'importance de ce phénomène.

Un nombre important de travaux scientifiques a été consacré au rapport entre l'approvisionnement en eau et le rendement de la plante, mais la plupart étudient les plantes cultivées dans des conditions d'irrigation. D'autre part, des connaissances utiles sur l'adaptation de cette culture à des conditions tropicales limitées et surtout pour ce qui concerne l'approvisionnement en eau, sont rares et fragmentaires. Dans cet article, nous avons essayé de déterminer l'état de la recherche en ce qui concerne la stratégie nécessaire à l'amélioration de la résistance du tournesol à la sécheresse et nous avons tenté, en même temps, d'identifier, parmi ses nombreuses caractéristiques agronomiques et ses paramètres physiologiques, celles et ceux qui pourraient être utilisés pour améliorer l'efficacité du processus de sélection.

Pour établir un programme génétique destiné à améliorer la résistance au stress dû à la carence d'eau, il faut tenir compte des points suivants:

- 1) Définition du type de milieu de sécheresse dominant dans la région ciblée pour chaque programme de culture, car différents types de sécheresse peuvent exiger différentes approches.
- 2) Dès que la région ciblée est clairement définie, définition des "idéotypes" de plantes.
- 3) Détermination des caractéristiques dont on croit qu'elles peuvent aider à la création d'espèces résistantes à la sécheresse.
- 4) Étant donné les conditions particulièrement difficiles et la nature inhabituelle des milieux sujets à la sécheresse, il est nécessaire de définir exactement la méthode de sélection et la conduite de l'expérience pour pouvoir orienter le choix (identification de la meilleure progénie) vers les données ayant un grand nombre de répliques plutôt que des valeurs uniques.
- 5) Des analyses de données qui permettent l'interprétation de l'interaction: génotype x milieu, surtout quand nous nous trouvons dans la situation d'identifier un seul génotype idéal pour différentes régions ayant des types différents de stress dû à la carence d'eau.

Ce n'est que quand on aura obtenu toutes les données pour chaque type de région et quand on les aura analysées d'une manière combinée ou-et séparée pour chaque type de milieu qu'il sera possible d'apporter une contribution concrète à ceux qui travaillent quotidiennement dans ces milieux difficiles et d'accélérer l'approvisionnement en matériel vraiment résistant au stress dû à la rareté de l'eau dans tous les milieux. Enfin, la technologie des marqueurs moléculaires pourrait faire surmonter les difficultés d'identification et de conduite de tests de résistance à la sécheresse.