

Prospects for the use of physiological traits during the selection for drought resistance in a sunflower population.

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Abstract

The use of physiological traits as a criterium for the selection of high-yielding sunflower genotypes subject to drought conditions has been proposed with the aim of evaluating (i) the presence of variability for selecting the above characteristics in the progeny population; (ii) the heritability and effectiveness of selection for these characteristics and (iii) which correlated responses are caused by selection for high physiological activity under drought in other growth traits. Carbon exchange rate, transpiration rate and leaf relative water content were used as selection criteria during a selection for improving drought resistance on a population coming from the start cross between a wild species *H. argophyllus* and a cultivated inbred line "C". Under drought conditions, F3 progeny was evaluated with other traits related to growth and yield, namely: flowering-maturity period, plant height, leaf area per plant, dry matter yield per plant and root/shoot index.

The variability expressed showed that a selection for the physiological traits was possible because of the absence of non-additive gene action. The heritabilities calculated as parent-offspring and as a standard unit were very similar and intermediate for all three characteristics, while the heritability produced, obtained by choosing the extreme values of the F2 population (divergent selection), was significantly greater than the others, showing the effectiveness of the physiological traits as selection criteria. Following a divergent selection on the F2 population, for elevated physiological activity under drought, involves obtaining genotypes with high vegetative growth and an elevated water consumption. This mechanism involved an increase of the root/shoot index and was very useful for the local pattern of water availability, enabling the stress by the maintenance of water uptake from deep wet soil layers to be avoided. While in correspondence of a selection vs. low physiological activity, the genotypes will show a more conservative mechanism to save water and limit their growth. This tolerance mechanism could be very useful in environments with superficial soil and with a fixed amount of water availability present at sowing time.

Key-words: drought improvement, physiological index, heritability, sunflower.

Introduction

The strategic approach in selections for drought resistance in a cultivated crop, reviewed by Blum (1980), such as that which involves the selective incorporation of specific morphological or physiological characteristics related to drought resistance, into varieties with high yield potential under optimum conditions has become a subject of major interest in recent years. Much of this interest is due to the time required for other selection criteria, that involve yield and its stability over many years and locations (Hurd, 1974; Hurd 1969; Fischer and Maurer, 1978), and to the progress on information about physiological processes and genetic system related to seed yield under drought conditions in sunflower (Feres *et al.*, 1986; Gimenez and Feres, 1986; Passioura, 1986; Turner, 1986; Baldini

et al., 1991). The identification of a simple physiological trait which confers an advantage to yield under a specific stress condition is a dilemma in many breeding programmes. Among the possible physiological mechanisms, gas exchange and leaf hydration are indicated by many authors (Boyer, 1976; Planchon, 1987) as being related to yield under drought and moreover permits reliable, effective and rapid measurements for screening the progeny.

The wild genetic resources of *H. argophyllus* have been used as a source of tolerance to drought in large programmes in many countries (Seieler, 1988; Skoric, 1992) and many of these studies have exclusively involved the variability on density of trichomes in the progeny in relation to physiological activity under wet and drought conditions (Harada and Miller, 1982; Iuoras and Voinescu, 1984; Blanchet and Gelfi, 1980; Morizet *et al.*, 1984); while Baldini *et al.*, (1993) and Martin *et al.*, (1992) suggest that the root system, instead of morphological leaf characteristics of wild species, could be responsible for a high physiological activity and high WUE under drought. In fact, even today there is no doubt that many shoot responses, such as leaf conductance, may arise from root signals as soil water status decrease and/or the resistance of the soil to root expansion increases (Tardieu and Davies, 1993; Passioura, 1988; Kramer, 1988; Passioura and Gardner, 1990; Tardieu, 1994).

The aim of this work is (i) to evaluate the variability of physiological parameters such as gas exchange and leaf relative water content in a population coming from the cross between *H. argophyllus* and a cultivated sunflower differing in the above characteristics under drought conditions; (ii) to estimate heritabilities from parent-offspring regression of advanced filial generations, (iii) to determine the effectiveness of selection for the above physiological characteristics during the selection and measure the possible effects of this selection on other traits related to plant growth and yield.

Materials and Methods

A single-cross population was used in this study. The parents of the population were the wild species *H. argophyllus* coming from USDA-ARS, North Dakota as the male parent and characterised by good physiological behaviour under drought as previously reported by Baldini *et al.* (1993) and, as the female, the C line a cultivated modern inbred line, selected at the Pisa University Agronomy Department and chosen because of its susceptibility to drought (Baldini *et al.*, 1993). The parents were crossed during the summer of 1991 and the F₂ generation was produced by controlled selfing of six F₁ plants under warm and illuminated conditions in a greenhouse during the winter of 1992. The F₃ generation was also obtained by selfing and harvesting the F₂ plants separately.

Single-plant evaluation in the field

The two parental genotypes and the F₂ plant generation were evaluated in the field under drought conditions during the summer 1992 at the Pisa University Experimental Farm, located at San Piero a Grado, 10 km from Pisa, on a homogeneous deep soil with a sandy loam texture and where the ground water level, during the study period was about 2.5 to 3 m below soil surface. The two parental lines and the 156 F₂ seeds from the population were sown on 5 June 1992 in six adjacent rows 7 m long with 0.7-m separating them at a rate of about 4 seeds m⁻². Border rows were established. 70 kg P₂O₅/ha and 80 kg N/ha was applied to the experimental plots and all the phosphate fertiliser was applied at sowing while nitrogen was applied on two occasions, 50% at sowing time and 50% 21 days after emergence. The emergence of the plantlets was favoured by two irrigations, the first immediately after sowing and the second 4 days after, consequently the F₂ progeny had definitively emerged 10 days after sowing time and was composed of 144 plants. After

the emergence, irrigation was interrupted and the plants were grown under drought to maturity and no significant rainfall occurred during the crop cycle. 65 days after sowing (incipient flowering time), the following characteristics were recorded:

- gaseous exchange of the plants as Carbon exchange rate (CER) ($\mu\text{mol m}^{-2} \text{sec}^{-1}$) and Transpiration rate (TR) ($\text{mmol m}^{-2} \text{sec}^{-1}$);
- Relative leaf water content (RWC) (%).

Leaf gas exchange was measured between 1 h prior to and 1 h after solar noon, using a commercial ADC (Analytical Development CO., England) open-portable system (Long and Hallgren, 1985). All measurements were made in the midsection of three top fully expanded leaves for each plant; from the same leaf per plant on which values of gaseous exchange were obtained, the relative water content of the leaves (RWC) was sampled during the same afternoon (at about 17.00 local STD time), following the methodology suggested by Sobrado and Turner (1983).

All 144 F3 progenies, derived from each selfed F2 plant, were evaluated under a rainout shelters during the summer of 1993 at the Pisa University Experimental Farm. The plants were hand sown on 2nd June and the soil was maintained at approximately field capacity until 40 days after sowing. Later, drought conditions were imposed by suspension of irrigation, resulting in a progressive water stress until physiological maturity. Each progeny was arranged in single adjacent rows, 2 m long with a 0.5-m row spacing with a final number of 8-10 plants per plot, following a randomised block experimental design, with two replicates. 72 days after sowing, the same physiological characteristics mentioned above were recorded in all plots and in addition the following parameters were measured:

- leaf area per plant (L.A) (dm^2), calculated using the relationship followed by Rowson *et al.*, (1980);
- flowering-physiological maturity period (F-M), (days);
- plant height (H) (cm);
- aerial dry matter per plant (g);
- root dry matter per plant (g);
- root index.

At maturity four plants per plot were harvested by hand and subdivided into above-ground matter and root and dried at 80°C before weighing. Care was taken when pulling plants to recover as much of the root system as possible, digging up a soil volume 60 cm deep and 30/30 cm area through the crown of each plant. Root index was calculated as the proportion of root dry matter in the total dry biomass.

Heritability estimation

Narrow-sense heritability for the physiological characteristics was estimated using simple linear parent offspring regression. F3 progeny means obtained in 1993 under rainout shelters were regressed separately on individual F2 parent plant values, coming from the field during 1992. Parent-offspring regressions were adjusted for parental inbreeding according to Smith and Kinman (1965) and the regression coefficients and their standard errors were multiplied by 2/3. Since parents and progeny were evaluated in different environments and years, heritability cannot be influenced by the 'genotype x environment' interaction (Casler, 1982). Nevertheless, different environmental conditions which tend to interact with the phenotypic expression of the plants could change in scale from parents to progenies with a drastic effect on the magnitude effect of heritability estimate (Frey and Horner, 1957). To reduce the potential scale effect of the two environments, the correlation coefficient was also used as an estimate of heritability, which is equivalent, as reported by Frey and Horner (1957) to the regression coefficient on data coded in terms of standard deviation units (standard-unit heritability).

Selection

At the same time, seeds from 12-13 F2 plants of each physiological characteristic (CER, TR and RWC) exhibiting the highest and lowest values (positive and negative selection) were chosen and grown randomly within the same experiment as described for the F3 progenies. The average F2 selection intensity was 17.3% for RWC and CER and 18.7% for TR. A heritability obtained (Hr) was also estimated using the results of F3 progeny values as a consequence of selection among the F2 plants using the formula suggested by Farnham *et al.*, (1990) :

$$Hr = \frac{[(\text{mean of selected F3 progenies}) - (\text{F3 mean population})]}{[(\text{mean of selected F2 plants}) - (\text{F2 mean population})]}$$

The effect of the divergent selection for the above three physiological characteristics on the expression of other related growth-yield characteristics on F3, was also evaluated using correlation analysis. Family means of possibly associated other traits on the F3 progeny generation, were regressed on the three characteristics CER, TR and RWC of individual F2 parents in the previous generation in order to determine if other characteristics were altered by the selection for extreme positive or negative levels of physiological activity under drought.

Results and Discussion

The distribution for the three physiological characteristics (CER, TR and RWC) in the F2 population was unimodal and continuous for all characteristics, as shown in Fig. 1. For all characteristics, some plants of the F2 population exceeded the mean value of the wild parent and the number of individuals which had lower values than the cultivated parent (C line) was greater than the number that showed higher values than the wild parent, especially for CER and TR characteristics, exhibiting a transgressive segregation. The distributions were observed to be slightly skewed towards higher values for CER. In any case, the F1 means did not show values higher or lower than the midparent values excluding non-additive gene action for all traits, confirming the possibility of obtaining some results in adopting a breeding selection programme.

Analysis of variance of all F3 progenies, reported in Table 1, showed significant differences between progenies for all the characteristics examined, underlining the presence of high variability in the F3 population, although cultivated under drought conditions. The levels of the plants stress expressed as water potential pre-dawn (data not shown) were between -0.75 and -2.1 Mpa in the F2 trial and between -0.8 and -2.5 Mpa in the F3 trial.

Heritability estimates computed using the F3-F2 linear regression (Tab. 2) were low for TR ($h^2=0.28$) and intermediate for CER and RWC ($h^2=0.37$ and 0.36 respectively). Since the parents and offspring were cultivated in different environments, heritability estimates with the regression coefficient as reported above, would not be biased by a 'genotype x environment' interaction (Casler, 1982), but possible interferences on the heritability estimate could be due to scale differences by different environmental effects on some plants characteristics (Fernandez and Miller, 1985; Casler, 1982). For this reason, computation of heritability in standard units was performed and is reported in the same tab. 2. The similarities of estimates between the two heritabilities suggests the absence of significant scale differences between offspring and parents and this fact may be explained by the possibility that both progenies showed the same reaction mechanism even if under the different environmental conditions of drought.

The estimation of the heritability obtained (H_r) from a divergent selection with an intensity of about 17-18% on the F2 population was similar in both positive and negative selections for TR (0.49 and 0.48 respectively) and for RWC (0.73 and 0.72 respectively), while the heritability obtained in negative selection for CER showed a significantly higher value than the positive selection (0.82 and 0.64 respectively) (Tab. 3). This result was probably due to the presence, during inbreeding, of few F2 plants with stable and conditional chlorophyll mutants with altered leaf pigmentation (Mihaljcevic, 1992a, b) which inhibit the photosynthetic activity even in their progenies. However, these estimations were significantly higher in magnitude than the regression obtained from an unselected population and suggested that the effectiveness of the selection under drought conditions for the above characteristics could be significantly improved by choosing extreme values.

The correlated responses between the physiological characteristics used as selection criteria during the selection and the other characteristics analysed on the derived F3 progeny resulting from a divergent selection on the basis of F2 plant population performance were calculated. As reported in tab. 4, there were only statistically significant correlations, with many high r values and there were no negative correlations between F2 physiological traits and the measured yield/growth characteristics of the derived F3 progenies. These results indicate that correlation coefficients were higher for CER than with respect to TR and RWC in correspondence with plant height ($r=0.78$), flowering-maturity period ($r=0.75$), plant leaf area ($r=0.75$) and aerial plant dry matter ($r=0.73$). A small but highly significant correlation was however obtained between F3 root dry matter and root/shoot ratio and physiological characteristics in the F2 stock. Thus the selection in the progeny, under drought conditions and especially for elevated CER, determined a lengthening of the reproductive period and an increase in plant height, in leaf area per plant and generally in plant dry matter with the root system increasing more than the aerial part.

Conclusions

The results obtained in these studies indicate that reasonable selection progress would be expected for RWC and CER, especially when applied under drought conditions, as selection criteria to segregating populations coming from the above described parental materials: a wild species, *Helianthus argophyllus*, and a cultivated inbred line. The absence of detectable, non-additive, genetic effects for these physiological traits suggests that selection might be practised as early as the F2 generation on the basis of performance of individual plants and that the effectiveness of the selection could be significantly improved by choosing the extreme values of the population. The results obtained from the correlated responses of the other traits allow some considerations on the use of physiological traits for the selection of drought-resistant genotypes. Selecting for extreme values of gas exchange and RWC under limited water availability has produced genotypes which have activated opposite mechanisms to resist drought. In fact, the genotypes selected for elevated physiological activity had a high vegetative growth, large leaf area per plant, elevated transpiration rates per unit leaf area and consequently an elevated water consumption per plant (Tab. 4). The mechanism involved, probably coming from the wild species (Baldini *et al.*, 1993), enables stress to be avoided by an increase in the root index (Tab. 1 and 4) with a bigger soil volume explored by deep roots, permitting the maintenance of water uptake. The appropriateness of this selection strategy that might be confirmed by positive yield results in the future, and could be emphasised in an environment such as that used in this trial, characterised by a very deep non-compacted

soil with a favourable structure and with deep wet layers below 2-3 m. Under different environmental conditions, characterised by a very thin superficial soil, rich in structural obstacles such as stones or in the presence of very compacted soil, with a fixed and limited water availability at sowing time, probably the genotype selected above wasted all the water during the vegetative phases, with a very negative influence on the final yield. A genotype more adapted to this environment could probably be obtained from the negative extreme values of the population under selection, with a more conservative mechanism with limited gas exchange, water consumption and a reduced growth, in which hormonal messages from roots under drying soil, become predominant in reducing both physiological activity and growth of the plants (Tardieu, 1994). For these reasons, the physiological traits utilised as indices during a selection programme to improve drought resistance could be very interesting even because they are somewhat heritable and screened without sophisticated technology, but the importance of local patterns of water availability, related to environmental conditions, seems fundamental in the determination of traits contributing to drought tolerance.

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Tab. 1 - Analysis of variance for all analyzed characters on F3 progeny grown under limited water availability, 1993.

Sources of variation	d.f.	CER	TR	RWC	flow-mat period	plant leaf area	plant height	plant dry matter	root dry matter	root/shoot ratio
<i>Mean squares</i>										
blocks	1	13.7	0.9	0.00006	34.1	71.1	27.3	1214.4	30.4	0.00084
F3 families	172	100.5**	4.3**	0.015**	83.9**	7547.1**	13864.2**	49689.2**	1036.3**	0.0033**
Error	172	12.6	0.8	0.001	11.6	170.9	317.6	1409.9	31.3	0.0007

*,** Significant at P ≤0.05 and ≤0.01, respectively

Tab.2 - Estimation of heritabilities (± SE) as regression coefficient (h^2a) and as standard unit (h^2b) from linear regression of physiological parameter means of F3 progeny on physiological values of individual F2 parents.

Characters	$h^2 a$	$h^2 b$
CER	0.37 ± 0.06	0.42 ± 0.06
TR	0.28 ± 0.07	0.32 ± 0.08
RWC	0.36 ± 0.06	0.39 ± 0.08

Tab. 3 - Estimate of realized heritability (H_r) for physiological parameters computed from family mean of F3 progeny of divergent selections among F2 plants.

Characters	H_r	
	positive	negative
CER	0.64	0.79
TR	0.49	0.48
RWC	0.73	0.72

Tab. 4 - Regression coefficient of mean values of growth-yield traits of F3 progeny on physiological characters of individual F2 parents grown the previous year and obtained by divergent selection.

Characters	flow.-matur. period	plant leaf area	plant heigh	plant dry matter	root dry matter	root/shoot ratio
CER	0.75**	0.78**	0.75**	0.73**	0.65**	0.50**
TR	0.72**	0.69**	0.67**	0.63**	0.53**	0.40*
RWC	0.60**	0.55**	0.71**	0.53**	0.52**	0.44*

*,** Significant at $P \leq 0.05$ and ≤ 0.01 , respectively

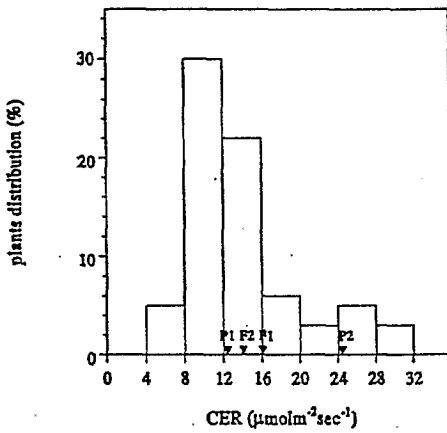


Fig.1 - Distribution of F2 plants for Carbon Exchange Rate (CER).

F2=F2 mean; F1=F1 mean; P1=mean of cultivated parent; F2=mean of wild parent

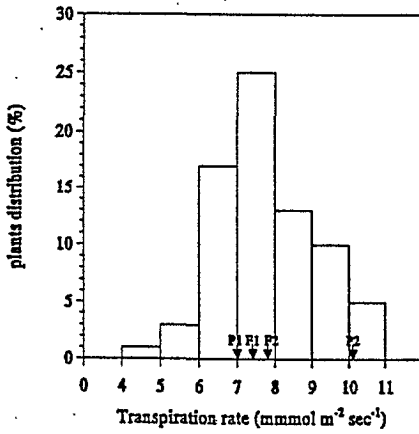


Fig.2 Distribution of F2 population for Transpiration rate.

F2=F2 mean; F1=F1 mean; P1=mean of cultivated parent; P2=mean of wild parent

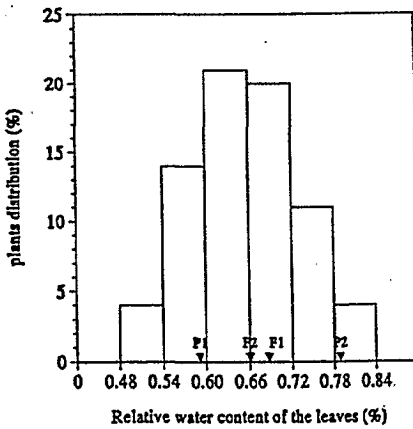


Fig.3 - Distribution of F2 population for Relative Leaf Water Content