Exploring genotypic strategies for sunflower drought resistance by means of a dynamic crop simulation model

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ABSTRACT

Although sunflower is often reported as a drought-tolerant crop, it suffers from intense and frequent periods of water deficit in Europe because it is mostly grown on shallow soils, under low rainfall and in rainfed areas. Given the limitations of experimental trials to explore a large number of drought scenarios, a dynamic crop simulation model was developed to determine different phenological (duration of post-anthesis period), morphological (leaf area) and physiological (rate of stomatal closure) putative traits of drought resistance in sunflower. A virtual experimental network was built by combining 4 locations (N-S gradient), 3 soil depths, over 36 weather seasons. In each of the 432 trials, 12 synthetic varieties were evaluated, differing by earliness at maturity (2 levels), leaf area (3 levels), leaf expansion and stomatal regulation sensitivity to progressive soil drying (2 levels: early or late response). This simulation study suggests that the varieties with early stomatal closure could result in the best yields in drought-prone environments, this trait being more determining than leaf area or earliness. In the most productive locations, late varieties, with large leaf area and late stomatal closure should result in the best yield. It is concluded that an additional variety screening including the response to water deficit could improve the choice of optimal sunflower cultivars in France.

Key words: drought resistance – leaf area – phenology – simulation model – stomatal regulation – varietal choice.

INTRODUCTION

Sunflower (*Helianthus annuus* L.) is often reported as a drought-tolerant crop (Unger, 1990; Connor and Hall, 1997). However, in southern Europe it suffers from intense and frequent periods of water deficit because it is mostly cultivated in low rainfall areas, without irrigation, and on shallow soils.

Ludlow (1989) reviewed three main genotypic adaptations to water-limited environments: (a) drought escape, whereby the crop completes its life (or oversteps a critical growth stage) before the onset of severe drought, (b) drought avoidance, where the crop maximizes its water uptake and minimizes its water loss, and (c) drought tolerance, where the crop continues to grow and function at reduced water contents. To these plant strategies, crop management offers additional opportunities (Debaeke and Aboudrare, 2004): (d) drought alleviation or moderation, by the means of irrigation, (e) optimal crop water use pattern, by reducing soil evaporation and increasing the contribution of transpiration during grain filling period (through crop density and N fertilization).

In commercial fields, drought resistance should be achieved by combining optimal cultivar choice and crop management. But limited information is available to characterize the response of sunflower cultivars to water stress, as drought resistance is a complex trait which cannot be evaluated accurately at field level. Field trials where water deficit occurs are generally banned from the official evaluation network because of poor statistical value.

Given the limitation of experimental trials to explore a large number of drought scenarios, dynamic crop modelling may be an alternative to arduous experimentation and is recognized as an adequate tool to identify genotype x environment x cultural practice combinations to achieve the most stable yield over a wide range of soil water availabilities (Agüera et al., 1997; Sinclair and Muchow, 2001; Chapman et al., 2002; Soriano et al., 2004).

Although several models are available for sunflower crop (e.g. Chapman et al., 1993; Villalobos et al., 1996; Pereyra-Irujo and Aguirrezabal et al., 2007), a new simulation framework was developed to represent more explicitly the varietal differences and to support cultivar choice decision in relation with water availability (Casadebaig, 2008). The main original point comes from using genotypic parameters that are measured directly from field or greenhouse trials.

The objective of this communication is to examine, by means of this dynamic simulation model, whether different varietal types defined by earliness, architecture, and response to soil desiccation should be recommended in France over the sunflower production area when natural water availability (precipitation, soil depth) is changing.

MATERIALS AND METHODS

Model and varietal parameters

The simulation model equations are described in detail in Casadebaig (2008): the daily step model simulates dynamically achene yield and oil concentration as a function of classic weather data (temperature, precipitation, ET_{ref}), soil data (available soil water content, N mineralization), crop management (sowing date, plant density, N fertilization, irrigation) and varietal characteristics (phenology, leaf area dynamics, leaf expansion and transpiration rate response to soil water deficit, biomass allocation).

Phenological parameters are: growing degree days (Tbase: 4.8°C) to reach different characteristic growth stages: emergence (A2), star bud (E1), early anthesis (F1), early grain filling (M0), physiological maturity (M3).

Leaf area (LA) index evolution is simulated on an individual leaf scale basis (Lizaso et al., 2003) and modulated from the measurement of 3 architectural parameters at anthesis: total leaf number, position and length x width of the largest leaf.

The extinction coefficient (k) is determined either directly or through a statistical adjustment using the previous LA parameters.

Genetic harvest index and oil concentration are determined in dense and unstressed sunflower stands.

Modules for development, biomass accumulation and allocation to the achenes were built using robust representations from the literature.

An original screening method was developed in greenhouse to parameterize leaf expansion and stomatal closure response to soil water content. Thresholds were calculated for a range of genotypes from different sources of selection (Casadebaig et al., 2008).

Phenotypic database

A database was built to gather the results of numerous experiments conducted by INRA and Cetiom from 2001 to 2007 on sunflower phenotyping (Debaeke et al., 2004). More than 20 cultivars representing the genetic progress from 1960 onwards (Vear et al., 2003) were fully described.

A virtual multi-environment trial network

From the phenotypic database, 12 virtual cultivars (Table 1) were created by combining 2 variants of earliness (E, early: 1750 °C.day from A2 to M3; L, late: 2160°C.day), 3 levels of plant potential leaf area (S, small: 4000 cm²; M, medium: 8000 cm² ; L, large: 12000 cm²) and 2 extreme levels of plant regulation in response to soil drying (E: early control of leaf expansion and stomatal closure, at a relatively high soil water content ; L , late control, at a rather low soil water content) (Fig. 1). In this study, the term regulation was used to reflect the effects of both response traits (leaf expansion and transpiration control). It was assumed that all the characters of drought resistance were independent.

Table 1. Combination of the 3 phenological, morphological and physiological traits to build 12 virtual varieties

Variety	Code	Earliness	Leaf Area	Regulation
1	ESE	Early	Small	Early
2	ESL	Early	Small	Late
3	EME	Early	Medium	Early
4	EML	Early	Medium	Late
5	ELE	Early	Large	Early
6	ELL	Early	Large	Late
7	LSE	Late	Small	Early
8	LSL	Late	Small	Late
9	LME	Late	Medium	Early
10	LML	Late	Medium	Late
11	LLE	Late	Large	Early
12	LLL	Late	Large	Late

Four regions were selected to sample the main French sunflower cropping area: Midi-Pyrénées (South-West), Provence (South-East), Poitou-Charentes (Center-West) and Parisian Basin (Center-North). Each region was described by one climate station and 3 soil types. The following climate stations from INRA were chosen: Auzeville (Department 31), Avignon (84), Lusignan (86) and Versailles (78). Each climate series was composed of 36 x 365 daily recordings (1971 – 2006). Solar radiation and climatic water deficit were the highest in Avignon and the lowest in Versailles as expected.

The 3 soil types differing by soil depth and available soil water content (ASWC) were extracted from a soil data base from INRA (Brisson et al., 2006): S1 (ASWC: < 60 mm), S2 (80-120 mm), S3 (130-150 mm).

Sunflower crop management was the same in the 12 environments: sowing date on 20 April, 60 kg N/ha applied 15 days after emergence, no supplemental irrigation.

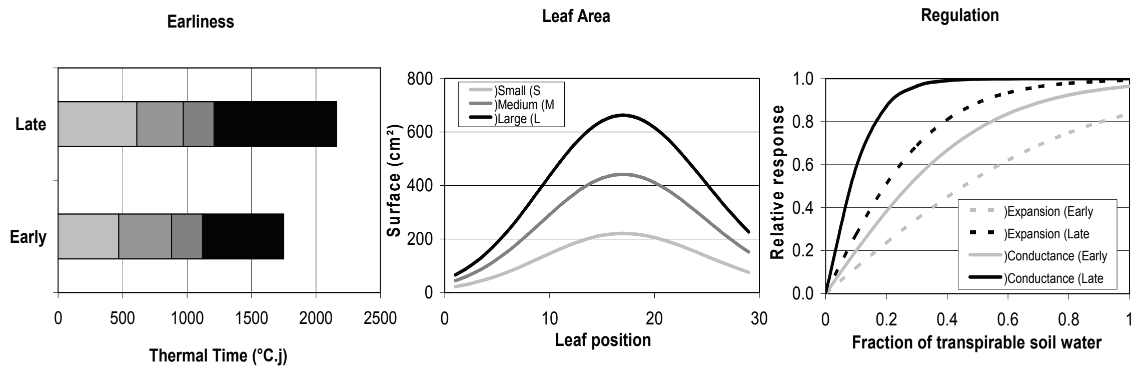

Fig. 1. Extreme values of phenological, morphological and physiological traits (maturity earliness, total leaf area, thresholds for stomatal closure and leaf expansion decline) among a range of 20 cultivars.

RESULTS

The application of the model resulted in different yield performances of the 12 varieties with season and pedoclimatic environment.

The northern situations (LUS, VER) resulted in higher yield levels, whatever the soil depth (Fig. 2). Grain yield was more stable in VER location (especially on S3) and more variable in Auzeville (AUZ). Average grain yield over 36 years ranged from 14 to 28 q/ha depending on soil type and climate. In France, average grain yield in national surveys ranges from 18 to 23 q/ha (at 0 % grain moisture).

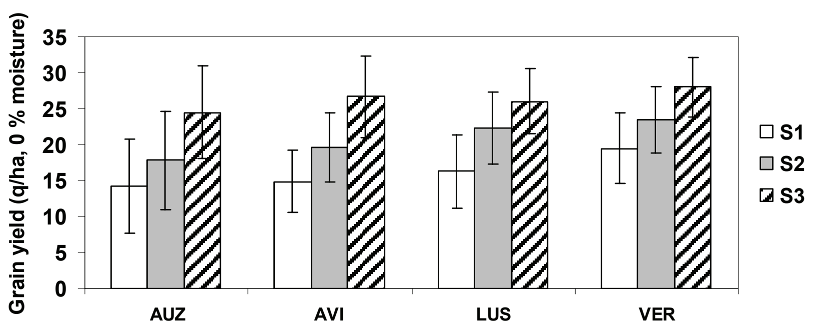

Fig. 2. Effects of location and soil type on grain yield (mean values and S.D over 36 years)
S1 = shallow ; S2 = medium ; S3 = deep soil

The mean effects of variety, earliness, leaf area and regulation on grain yield were displayed on Fig. 3. Late maturation, high leaf area index and early stomatal closure all increased grain yield: the latter trait was the most influential one (+ 3.8 q/ha vs 0.9-1 q/ha for the two other traits). The combination of the 3 traits resulted in GY variations from 18.8 (var. 2) to 24.4 q/ha (var. 11).

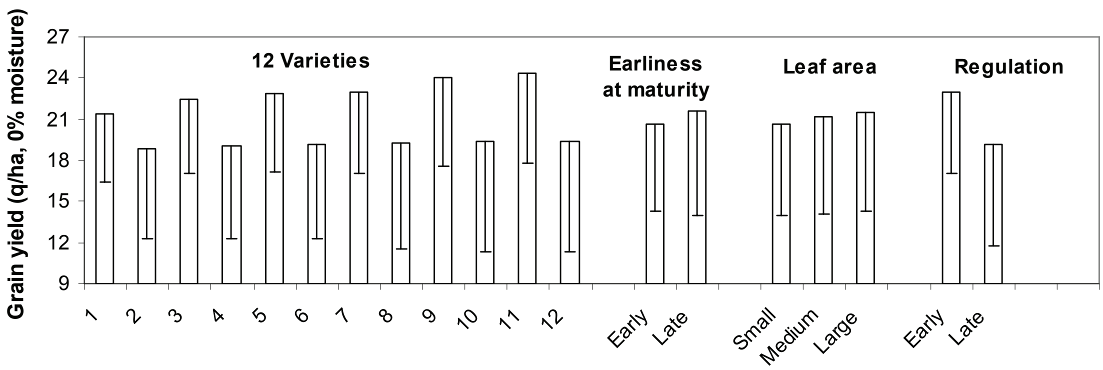

Fig. 3. Grain yield for the 12 virtual varieties and the 3 morpho-physiological traits (mean values and SD over 36 years)

The 3 traits (maturity earliness, leaf area, regulation) had a significant effect on yield (P < 0.001) but the 'trait x environment' interactions are not of the same level: highly significant for regulation (P < 0.001), significant at P < 0.1 for earliness, but not significant for leaf area.

To quantify the importance of a genotypic trait in a given location, an analysis of variance (ANOVA) was attempted as follows: Yield ~ Yr + E + LA + R + Yr*E + Yr*LA + Yr*R, in each environment (Table 2).

Table 2. Variances and statistical significance (*P<0.05; **P< 0.01; ***P<0.001) of the single effects (genotypic traits) and the 'year x trait' interactions in each of the 12 environments.

Location	Soil	Year (Yr)		Earliness (E)		Leaf Area (LA)		Regulation (R)		Yr x E		Yr x LA		Yr x R	
AUZ	S1	374	***	2	ns	12	***	4043	***	8.0	***	0.4	ns	19.8	***
AUZ	S2	376	***	7	*	2	ns	5574	***	5.3	***	0.7	ns	20.4	***
AUZ	S3	405	***	163	***	12	***	1757	***	8.9	***	2.3	***	37.7	***
AVI	S1	183	***	109	***	63	***	1089	***	2.4	***	0.3	***	8.3	***
AVI	S2	196	***	63	***	4	***	2633	***	2.4	***	0.5	***	4.9	***
AVI	S3	319	***	77	***	2	*	1885	***	9.7	***	2.8	***	8.3	***
LUS	S1	201	***	63	***	12	***	3283	***	7.6	***	0.7	ns	11.6	***
LUS	S2	211	***	87	***	2	ns	1850	***	7.3	***	1.0	ns	22.3	***
LUS	S3	185	***	249	***	22	***	753	***	5.0	***	1.1	*	19.2	***
VER	S1	217	***	90	***	82	***	996	***	6.2	***	1.7	**	24.0	***
VER	S2	204	***	112	***	60	***	364	***	7.1	***	4.3	***	19.1	***
VER	S3	156	***	567	***	407	***	33	***	3.9	***	1.5	***	1.9	***

If the advantage conferred by the R character was major whatever the environments (except for VER_S3 and VER_S2, where water stress was minimum), the impact of the other characters was dependent on the environment. Earliness (E) played a role in the medium and deep soils, where late varieties can take advantage of a longer growing duration. Leaf area, although its effect was significant in most of the environments, played only a significant role in the most extreme environments (AVI_S1, VER).

All the characters exhibited significant interactions with year, although Yr x R interactions were the most important. The existence of such interactions between the traits and the climate suggests that a varietal choice based only on the mean performance of a variety in a given location might be irrelevant in some years.

The R character was obviously the most determining one to explain yield variations in this simulation exploration: depending on the regions, regulation though leaf expansion and stomatal closure may be responsible for mean gaps of 7 q/ha in South-West (between varieties differing only by this character) but of 1.7 q/ha in the Parisian Basin region. These gaps were related to the intensity of soil water deficit, stomatal closure being a response to soil desiccation. Earliness had a lower influence: from 0.4 q/ha (South-West) to 1.8 q/ha (Parisian Basin). Concerning leaf area, the mean gap between two modalities ranged from 0.2 q/ha (South-West, Center-West) to 1.7 q/ha (Parisian Basin). Increasing LA had a negative impact on yield in the most drought-prone environments (AUZ, AVI) but only for varieties with late stomatal closure. The model suggested that « early regulation » has more impact than a variation in potential LA in these environments. In dry environments, reducing LA might not be a good strategy as potential yield would be reduced too much and soil evaporation could increase as well.

From the ANOVA, the best varietal choice (combination of 3 traits) among 12 candidates was determined for each of the 12 environments on the basis of 36 virtual trials (climate series) (Table 3).

At a regional level, the variety "11" or LLE (late maturing, large leaf area, early stomatal closure) would be systematically the best choice. The ideotype LLE was relevant 5 years out 10 in South-East and Parisian Basin and 7 years out 10 in the South-West and Center-West regions. Three years out of 10, the ideotype LLL, with late stomatal closure, would be a better choice in the Parisian Basin and the ideotype LSE, with a smaller LA, would be a better choice in South-East.

The soil type had no marked effect on the best choice within a region. But the frequency of the best yielding cultivar changed from one environment to another (from 46 % to 89 %). In general, early regulation should be recommended in shallow soils, because delaying soil water depletion in this way is a good strategy to sustain a large leaf area (and light interception). On the contrary, in the Parisian Basin region, in deep soils (VER_S3), where water deficit and global radiation are the lowest, the model selected a late maturing ideotype, with a late stomatal closure when exposed to water deficit (more photosynthesis in spite of more water transpired in the first part of the cycle) and a large LA value.

Table 3. Potential yield, mean GY value of the best ranked variety, and best ranked varieties in each simulated environment[1]

Location	Soil	Best year (q/ha)	Best variety (q/ha)	1st rank for variety n (%)	1st choice	2nd choice
AUZ	S1	27.0	18.0	71	**11** - 9 - 5	7 - 3 - 1
AUZ	S2	30.0	22.3	66	**11** - 9 - 7	5 - 3 - 1
AUZ	S3	34.1	28.1	63	**11** - 9	7 - 5 - 3
AVI	S1	25.4	17.7	89	**11**	9 - 5 - 3 - 7
AVI	S2	29.9	22.7	51	**11** - 9 - 7	5 - 3 - 1
AVI	S3	36.7	29.6	43	9 -11 - **7**	5 - 3 - 1
LUS	S1	26.4	20.4	83	**11** - 9	7 -5 -3 - 1
LUS	S2	30.9	25.7	66	**11** - 9 - 7	5 - 3 - 1
LUS	S3	33.1	29.0	71	**11** - 9	7 - 5 - 3
VER	S1	29.6	22.8	74	**11** - 9	5 - 3 - 7
VER	S2	32.6	26.0	46	**11** - 9	5 -7 - 3
VER	S3	35.0	30.5	63	11 - **12**	10 - 9

[1]The underlined variety number corresponds to the best ranked one in term of frequency over 36 years.

DISCUSSION

According to the model and to its multi-environment application, early regulation would be a relevant physiological trait to select in sunflower. According to Casadebaig et al. (2008), early stomatal closure is not frequent among commercial cultivars. This behaviour is closer to what is observed on isohydric species such as sorghum and maize. Conversely, Sinclair and Muchow (2001) did not simulate a significant increase in grain yield in sorghum, by manipulating this trait, as this crop was already well adapted to production under water stress.

In sunflower, changing cultivar earliness (from early to late type) did not result in huge differences in grain yield over the French cropping area, contrary to what is reported in Mediterranean environments (Debaeke and Aboudrare, 2004). In this paper, only differences in the anthesis-maturity were explored. The date of anthesis (about 10 days from early to late type) could have been modulated as well but probably with minor consequences on drought escape at anthesis. However, choosing an early maturing variety appeared as a good decision in the most stressful environments (AUZ_S1). Sowing date would probably have more effect on drought escape, especially sowing in autumn instead of spring as practised in the most southern regions of Europe (Soriano et al., 2004).

The optimal level of leaf area index results from a trade-off between transpiration, soil evaporation and light interception. In general, the lowest values of LA were not optimal in France even in the most stressed environments; plant density should rather be increased in this case.

Other traits have been reported as influencing grain yield in drought-prone environments: water extraction pattern and early vigour (Sadras and Hall, 1989; Agüera et al., 1997; Sinclair and Muchow, 2001). These traits could be explored by the model provided that experimental evidence of genotypic variation could be supplied.

The simulation of virtual genotypes, which is of interest for testing new combinations of traits, was based on characters expressing a sensitivity to water stress. From a practical angle, the farmer's decisions are based on cultivar potential productivity and disease tolerance (which were not considered in the simulations). Potential productivity corresponds to the LLL type in environments where water is not a limiting factor. With the exception of earliness, the characters involved in water stress resistance are not evaluated in the official trials and for that reason they cannot be exploited by the advisers. As cultivar choice results from a complex evaluation of a range of characters (some are measured, others result from expertise), the varietal supremacy of LLE type would be probably less visible in trials. The interaction with the weather may change the optimal choice. For that reason, 2 or 3 years of field evaluation as currently practised are not sufficient to explore the advantages and limits of a new variety. The simulation of varietal strategies may help the adviser to promote a cultivar with a stable yield over a wide range of pedoclimatic conditions.

ACKNOWLEDGEMENTS

Our partners CETIOM, ONIDOL, and OLEOSEM are gratefully acknowledged for their financial support and other facilities.

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