ENVIRONMENTAL ATTRIBUTES UNDERLYING ENVIRONMENTAL MAIN-EFFECTS AND GENOTYPE BY ENVIRONMENT INTERACTIONS IN SUNFLOWER

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Summary

In a previous study on 5 genotypic attributes of 10 sunflower hybrids in 21 environments, a wide range of mean yields and several patterns of genotype by environment (G×E) interaction were found. In this paper, environmental data are introduced as explanatory variables to allow the biological interpretation of the observed environmental main-effects and G×E interactions. Photoperiod, rainfall, maximum temperature and minimum temperature were computed for the different crop stages. Mean values of these variables for each crop stage were regressed on the environmental means and the environmental scores for the 1st and 2nd principal components of each genotypic attribute, to investigate the underlying causes of the variation in mean yields and the G×E interactions. A significant negative association between yield and rainfall between floral initiation and flowering was observed, which mainly affected grain number and grain weight. Minimum temperatures during the reproductive phenophases were also negatively associated with oil yield, mainly affecting grain weight and oil content. Photoperiod between floral initiation and flowering showed a positive correlation with oil yield. Correlations found between the environmental scores for the PCs for oil yield and the mean values of the computed environmental attributes for the different crop stages suggest that photoperiod and minimum temperature are the main environmental factors underlying the observed G×E interactions. These environmental factors affected the genotypic relative responses of all yield components. It is proposed that a hybrid adapted to the N mega-environment should improve its relative performance under short photoperiods and high minimum temperatures.

Introduction

Cultivars grown in multi-environment trials react differently to environmental variations. This differential response of cultivars from one environment to another is called genotype by environment (G×E) interaction. In Argentina, G×E interactions complicate effective identification of superior sunflower genotypes, such that relative cultivar yields vary across testing environments. In a companion paper (de la Vega *et al.*, 2000), we have used pattern analysis, i.e. clustering and ordination (Williams, 1976), to study the response patterns of oil yield and their components for a reference set of sunflower hybrids across a set of growing environments of Argentina. These analysis showed that the effects of northern (subtropical) and central (temperate) environments on genotype discrimination were orthogonal to opposite, indicating the existence of two mega-environments. When information of environmental variables is also available, these variables can be correlated to or regressed on the environmental mean scores and the environmental scores estimated by ordination analysis, to allow the biological interpretation of the environmental main-effects and the G×E interactions.

In this paper, environmental data are introduced as explanatory variables of the environmental and G×E effects found in the multi-environment trial described in de la Vega *et al.* (2000). The objective was to investigate the underlying causes of the observed variation in mean yields and G×E interactions.

Materials and Methods

The details of the experimental material, test environments, experimental design, measurements, analysis of variance, and pattern analysis are given in de la Vega *et al.* (2000). Average monthly values of four environmental attributes were used as potential explanatory variables of the environmental main-effects and the G×E interactions observed for oil yield and its components in the multi-environment trial described in de la Vega *et al*. (2000). As yield components (grain number, grain weight and oil content) are determined sequentially during the life cycle of the crop, with some overlapping between contiguous phases, we have computed the environmental attributes for the different crop stages. They were defined as early vegetative stage (E), late vegetative stage (L), anthesis (F) and grain filling (G). F was defined as 14 days around the mean date of full anthesis at each trial. The period between sowing and beginning of F was divided into two equal parts (E and L) which surrogate the phenophases sowing-floral initiation and floral initiation-first anthesis. G was defined as the period between the end of F and 35 days after full anthesis. Environmental variables computed for each crop stage were photoperiod, rainfall, maximum temperature, and minimum temperature. Mean values of these variables for each crop stage were regressed on the environmental mean scores (excluding managed-environments) and the environmental scores for the 1st and 2nd principal components (PC) of each genotypic attribute described in de la Vega *et al*. (2000), Table 2 and Figure 1.

Results

Environmental attributes underlying environmental main-effects

Mean oil yield across environments showed negative associations with rainfall between floral initiation and flowering (stage L, $P < 0.01$), and with minimum temperature between floral initiation and grain filling (L, F and G, $P < 0.05$), while it was positively associated to photoperiod between floral initiation and end of flowering (L and F, $P < 0.05$) (Table 1). Grain number m^{-2} was negatively associated with rainfall in stage L ($P < 0.01$). Grain weight showed negative associations with rainfall in L and G ($P < 0.01$) and with minimum temperature in stages L and F ($P < 0.01$), while it was positively associated with photoperiod in L and F ($P < 0.05$). Oil content was negatively associated with maximum temperature in E and G ($P < 0.01$) and to minimum temperature during all crop stages ($P < 0.01$), while it showed a positive association with photoperiod in L ($P < 0.05$), F and G ($P < 0.01$).

Table 1. Correlation between environmental means and four environmental factors and between the environmental scores for the 1st and the 2nd principal component and four environmental factors computed for four crop stages (E: early vegetative

stage, L: late vegetative stage, F: flowering, G: grain filling), for the ANOVA and principal component analysis of data from 10 sunflower hybrids grown in 21 environments of Argentina (de la Vega *et al*., 2000)

Env. factor	Oil yield			Grain number			Grain weight			Oil content		
	Env. mean	PC1	PC2	Env. mean	PC1	PC2	Env. mean	PC1	PC2	Env. mean	PC1	PC2
Rainfall												
E	0.39	0.29	-0.11	0.42	0.15	-0.11	0.33	0.08	0.34	0.29	0.10	0.22
L	-0.72**	-0.21	-0.02	-0.68**	-0.40	0.20	-0.64**	-0.08	0.01	-0.37	0.16	-0.20
F	-0.05	0.25	-0.50*	-0.03	-0.23	-0.02	0.09	-0.18	0.25	-0.10	0.21	0.22
G	-0.42	-0.13	-0.06	-0.37	-0.01	0.43*	-0.60**	0.16	0.09	-0.09	-0.01	-0.18
Maximum temperature												
E	-0.27	-0.53*	0.40	-0.06	-0.24	-0.45*	-0.29	-0.09	-0.21	-0.79**	-0.48*	-0.62**
L	0.17	-0.28	0.41	0.30	-0.06	-0.62**	0.12	-0.05	-0.20	-0.41	-0.36	-0.34
F	0.12	0.04	0.22	0.40	0.03	-0.37	-0.15	0.31	0.20	-0.33	0.06	-0.04
G	-0.19	-0.37	0.54*	-0.09	-0.05	-0.79**	-0.14	-0.14	-0.37	-0.66**	-0.01	-0.26
Minimum temperature												
E	-0.28	-0.64**	0.44	-0.14	-0.36	-0.27	-0.22	-0.29	-0.35	-0.71**	-0.57**	-0.73**
L	-0.52*	-0.74**	0.64**	-0.30	-0.19	-0.32	-0.60**	-0.23	-0.54*	-0.82**	-0.39	-0.76**
F	-0.49*	-0.36	0.22	-0.25	-0.32	-0.30	-0.53**	-0.14	-0.16	-0.74**	0.02	-0.36
G	-0.49*	-0.61**	0.62**	-0.37	-0.25	-0.56**	-0.40	-0.35	-0.60**	-0.74**	-0.05	-0.47*
Photoperiod												
E	0.42	0.28	-0.35	0.41	-0.03	0.13	0.40	0.05	0.43*	0.33	-0.13	0.12
L	0.50*	0.58**	-0.66**	0.43	0.04	0.27	0.48*	0.04	0.61**	0.52*	0.19	0.49*
F	0.56*	0.69**	-0.77**	0.42	-0.06	0.38	0.55*	0.02	0.57**	0.69**	0.42	0.66**
G	0.31	0.44*	-0.48*	0.08	-0.29	0.35	0.36	-0.02	0.23	0.63**	0.45*	0.46*

(* $P < 0.05$; ** $P < 0.01$)

Environmental attributes underlying G×E interactions

The environmental scores for the 1st PC for oil yield, which was positively associated to the central (C) environments (de la Vega *et al*., 2000, Figure 1A), showed negative associations with maximum temperature in E ($P < 0.05$) and with minimum temperature in E, L and G ($P < 0.01$), while they were positively associated to photoperiod in L, F ($P < 0.01$) and G ($P < 0.05$) (Table 1). This suggests that the hybrids which improve their relative performance in terms of oil yield in the C region, are responding positively in relative terms to photoperiod increases in L, F, and G, to maximum temperature decreases in E, and to minimum temperature decreases in E, L and G. The environmental scores for the 2nd PC, which was positively associated to the northern (N) environments (de la Vega *et al*., 2000, Figure 1A), showed a pattern of associations contrasting the scores for the 1st PC. They showed negative associations with rainfall in F ($P < 0.05$) and with photoperiod in L, F ($P < 0.01$) and G ($P < 0.05$) and positive associations with maximum temperature in G ($P < 0.05$) and minimum temperature in L and G ($P < 0.01$) (Table 1). The 2nd PCs for the three oil yield components (grain number, grain weight and oil content) appear to be related to the G×E interaction, and are positively associated to the C environments and negatively to the N environments (de la Vega *et al*., 2000, Figures1C, 1D and 1E). The environmental scores for the 2nd PC for grain number were positively associated with rainfall in G ($P < 0.05$) and negatively associated with maximum temperature in E ($P < 0.05$), L and G ($P < 0.01$) and with minimum temperature in G ($P < 0.01$). The environmental scores for the 2nd PC for grain weight were negatively associated with minimum temperature in L ($P < 0.05$) and G ($P < 0.01$) and positively associated with photoperiod in E ($P < 0.05$), L and F ($P < 0.01$) (Table 1), while the environmental scores for the 2nd PC for oil content showed a negative association to maximum temperature in E ($P < 0.01$) and to minimum temperature in E, L ($P < 0.01$) and G

($P < 0.05$) and a positive association to photoperiod in L ($P < 0.05$), F ($P < 0.01$) and G ($P < 0.05$).

Discussion

The results of these analyses contribute to the interpretation of the relationships between crop performance and environment from two angles. Firstly, they show major effects of environment. Thus, a significant negative association was observed between yield and rainfall from floral initiation to flowering, which mainly affected grain number and grain weight. This finding agrees with the results of Magrin *et al*. (1998), who analyzed the effects of ENSO on the productivity of grain crops in Argentina. The negative association between minimum temperature during the reproductive phenophases and oil yield (mainly attributable to responses of grain weight and oil content) is consistent with the findings of other authors (Rawson *et al*., 1984; Ploschuk and Hall, 1995; Villalobos *et al*., 1996). The positive correlation betwen oil yield and photoperiod between floral initiation and flowering is particularly interesting. This finding agrees with the hypothesis of Rawson *et al*. (1984), who suggested that the combination of short photoperiods and high temperatures experienced by sunflower crops in Northern Australia could partially underlie the low yields obtained in that region, at that time.

The second useful result of these analysis is the new light they shed on the connections between the G×E interactions and environmental attributes. Correlations between the environmental scores for the 1st and the 2nd PCs for oil yield and the mean values of the computed environmental attributes for the different crop phases suggest that photoperiod and minimum temperature are the main environmental factors underlying the observed G×E interactions. These factors affected the relative genotypic responses of all yield components. It is proposed that a hybrid adapted to the N mega-environment should improve its relative performance under short photoperiods and high minimum temperatures, and a C-adapted hybrid should improve its relative performance under long photoperiods and low minimum temperatures, particularly when these conditions apply during the reproductive phenophases. We are not aware of any previous information on the effects of photoperiod on yield and yield components in sunflower. Responses of this type have, however, been found for peanut (Bagnall and King, 1991; Bell and Wright, 1998) and cowpea (Hall, 1992; Ehlers and Hall, 1998). These authors found that photoperiod differentially affects biomass partitioning to reproductive structures and it was established that the expansion of these crops towards other latitudes would be associated with breeding for genotypic adaptation to the photoperiodic regime during reproductive stages. While there is some information about temperature effects on sunflower yield and its components (e.g. Downes, 1975; Dompert and Beringer, 1976; Harries *et al*., 1982; Rawson and Hindmarsh, 1982; Rawson *et al*., 1984; Ploschuk and Hall, 1995; Villalobos *et al*., 1996), there is almost no published data about intraspecific variability in the responses to this environmental factor, except for a study on the membrane thermostability as a heat tolerance associated trait (Balota, 1994). A final interesting aspect of these G×E/environment connections is the apparently greater effect of rainfall during flowering on N-adapted hybrids. Finally, we note that we were unable to explore the connections between radiation regime and G×E effects and emphasize the need to extend these analyses to include the treatment of this environmental variable.

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