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Genotype by environment interaction and indirect selection for yield in sunflower

II. Three-mode principal component analysis of oil and biomass yield across environments in Argentina

Abelardo J. de la Vega[a,*], Scott C. Chapman[b]

[a]*Advanta Semillas S.A.I.C., Ruta Nac. 33 Km 636, CC 294, 2600 Venado Tuerto, Argentina*
[b]*CSIRO Plant Industry, Long Pocket Laboratories, 120 Meiers Road, Indooroopilly, Qld 4068, Australia*

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Abstract

The genotype by environment (G × E) interactions observed for sunflower oil yield in different regions of Argentina can be analyzed in terms of differences among genotypes in individual environments for its components grain number, grain weight, and oil content (yield analysis). Similarly, G × E interactions observed for oil-corrected grain yield can be analyzed in terms of its determinants total biomass and harvest index (physiological analysis). Three-mode (genotypes × environments × attributes) principal component analysis was applied to $10 \times 21 \times 4$ and $10 \times 11 \times 3$ matrices, for each of the first and the second analyses, respectively, to collectively interpret the changes in these attributes in a sunflower genotype–environment system, and to assess the relative importance of each trait as underlying determinant of the observed G × E interaction for oil yield. The $3 \times 2 \times 3$ and $4 \times 4 \times 2$ (genotypes × environments × attributes) principal component models explained about 65% of the variation computed for first and second approaches, respectively.

For the yield analysis, the first environment component (54% of the variation) explained the common pattern of oil yield over environments and showed that oil content was highly positively correlated to oil yield, while grain number and grain weight showed lack of association with oil yield and were negatively correlated. The second environment component (11% of the variation) contrasted northern and central environments and showed that grain number is the main underlying determinant of the observed G × E interactions between these two mega-environments for oil yield.

In the physiological analysis, the first environment component (29% of the variation) explained the common pattern of oil-corrected grain yield over environments and showed that harvest index was more strongly positively correlated to oil-corrected grain yield, but not to total oil-corrected biomass. The second environmental component (19% of the variation) contrasted northern and central environments and showed that oil-corrected biomass is the physiological attribute that is largely responsible for the G × E interactions for oil-corrected grain yield.

Keywords: Adaptation; Determinants of yield; G × E interaction; Three-mode principal component analysis; Sunflower

1. Introduction

In Argentina, effective identification of superior sunflower (*Helianthus annuus* L.) genotypes is complicated

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[*] Corresponding author. Tel.: +54-3462-435-235;
fax: +54-3462-435-231.
E-mail address: avega@waycom.com.ar (A.J. de la Vega).

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by the presence of significant genotype × environment (G × E) interactions, such that relative cultivar yields vary across testing environments (de la Vega et al., 2001). G × E interaction introduces uncertainty into the selection process when it reduces the genotypic correlation among environments in the way in which they discriminate among the genotypes (Cooper and DeLacy, 1994). These interactions reflect differences in genotype adaptation which may be exploited by selection and by adjustments in the testing strategy (Basford, 1982). Testing regimes may ignore, avoid, or exploit G × E interactions (Eisemann et al., 1990). Ignoring the G × E interactions is to consider them as a source of error or bias in assessing a genotype. To avoid or exploit them, consider the G × E interactions as a component of variation, which is, in part, heritable and exploitable through selection for broad or specific adaptation (Cooper and Fox, 1996). An objective decision between breeding for broad adaptation (minimizing interactions) or specific adaptation (emphasizing favorable interactions) requires a full understanding of the nature of such interactions (Basford, 1982).

In a previous paper (de la Vega et al., 2001), we have used two-way multiplicative models, i.e. pattern analysis (Williams, 1976), to study the response patterns of oil yield, yield components, and yield determinants for a reference set of sunflower hybrids across a set of growing environments of Argentina. These analysis showed that: (i) the effects of northern (subtropical) and central (temperate) environments on genotype discrimination were strongly orthogonal, indicating the existence of two mega-environments, and the possibility of selecting for specific adaptation; (ii) delayed planting dates in a central location were positively correlated with the northern environments, representing an opportunity to exploit indirect responses to selection; (iii) some hybrids with similar patterns of relative oil yield across environments showed contrasting response pattern when considering yield components individually, which suggested the existence of different specific genotypic responses to specific environmental challenges within the same genotype groups for oil yield, i.e. there were different ‘pathways’ by which similar oil yields could be achieved across environments.

Oil yield can be analyzed as the product of its components (grain number, grain weight, and grain oil percentage). It can be also viewed as the product of biomass production and harvest index. Thus, the G × E interactions observed for sunflower in different regions of Argentina can be analyzed in terms of differences among genotypes in individual environments using two different yield analysis frameworks: (i) yield components: grain number, grain weight, and oil content or (ii) yield determinants: total biomass yield and harvest index. In sunflower, the genotypic and environmental effects on seed oil content may confound the interpretation of trial results for crop biomass and harvest index. Thus, for comparative purposes, crop biomass measurements should be corrected for energy expended in oil synthesis.

Where more than one attribute is measured on genotypes in multi-environment trials, the collected data can be summarized in the form of genotype by environment by attribute (G × E × A) array of means (Basford et al., 1996). In this case, the generalization of two-way multiplicative models to three-way multiplicative models is a useful strategy for the simultaneous modeling of G × E interaction in more than one trait (van Eeuwijk and Kroonenberg, 1995), and has been successfully used for studying multi-attribute genotypic responses across environments (e.g. Kroonenberg and Basford, 1989; Basford et al., 1990; Chapman et al., 1997).

In this paper, three-mode (genotypes × environments × attributes) principal component analysis (Kroonenberg, 1983) was applied to $10 \times 21 \times 4$ and $10 \times 11 \times 3$ matrices, for the first and the second yield analysis frameworks, respectively, to collectively interpret the changes of these attributes in a sunflower genotype–environment system, and to assess the relative importance of each trait as an underlying determinant of the observed G × E interaction for oil yield.

2. Materials and methods

2.1. Trial data set

The details of the experimental material, test environments, experimental design, and measurements are given in de la Vega et al. (2001). A reference set of 10 sunflower single cross-hybrids was evaluated in 21 central, northern, and managed environments of

Argentina during the 1996/1997 to 1998/1999 seasons (Table 1), to identify patterns of G × E interaction and opportunities to exploit indirect responses to selection. The hybrids composing the reference set of genotypes were selected from the Advanta Argentina testing program on the basis of their contrasting relative performance across environments and also because they represent a wide range of genetic diversity according to RFLP (restricted fragment length polymorphism) molecular marker analyses (A. Leon, Advanta Argentina, Balcarce, unpublished data).

The locations ranged from 23 to 37°S, and are evenly distributed between subtropical (northern) and temperate (central) sunflower-growing environments. Three of the 21 were managed environments. In V27, V29, and VI9, the normal October planting date for central locations was delayed until December and in VI9 the day length was artificially extended to 15.5 h during the whole crop cycle. In each environment, a randomized complete block design with three reps was used to test the 10 genotypes.

Plot data for oil yield, grain number per square meter, 1000 grain weight, and oil content were recorded for all trials (Table 1). Yield and yield components were determined by hand harvesting of the central row of each plot, discarding the border plants. Grain weight was determined by weighing and averaging three random samples of 100 achenes per replication and the number of grains per square meter was calculated from the grain yield. Oil content was determined by nuclear magnetic resonance (Granlund and Zimmerman, 1975). For three-mode multivariate analysis, the collected data was summarized in the form of a 10 × 21 × 4 (G × E × A) array of means.

Plot data of oil-corrected grain yield, total oil-corrected aboveground biomass yield, and harvest index were recorded for 11 trials (Table 2). Aboveground biomass was sun-dried in a glasshouse at 50–60°C for more than 5 days. Aboveground biomass and grain yield measurements were corrected for oil synthesis costs using the production values given by Penning de Vries et al. (1983) as explained in de la Vega et al. (2001). The results are termed oil-corrected biomass and oil-corrected yield in this paper. Harvest index was calculated as the ratio of oil-corrected yield to oil-corrected biomass. For three-mode multivariate analysis, the collected data was summarized in the form of a 10 × 11 × 3 (G × E × A) array of means.

Three-mode principal component analysis (Kroonenberg, 1983) was used for studying the genotype × environment × attribute matrices.

2.2. Three-mode principal component analysis

This procedure derives components for each of the three modes (say P, Q, R components for genotypes, environments, and attributes, respectively), as well as a three-way matrix of order P by Q by R (the core matrix). In this model, each mode is allowed to have a different number of components. The core matrix contains the weights assigned to each of the combinations of the components for the three modes. The complete model is written as (Kroonenberg and Basford, 1989; van Eeuwijk and Kroonenberg, 1995)

$$x_{ijk} = \sum_{p=1}^{P}\sum_{q=1}^{Q}\sum_{r=1}^{R} a_{ip} b_{jq} c_{kr} g_{pqr} + e_{ijk}$$

where a_{ip} represents the coefficient for genotype i in the genotypic component p $(p = 1, \ldots, P)$, b_{jq} the coefficient for environment j in the environmental component q $(q = 1, \ldots, Q)$, and c_{kr} the coefficient for trait k in the trait component r $(r = 1, \ldots, R)$. The term g_{pqr} indicates the joint weight for the pth component of the genotypic mode, the qth component of the environmental mode, and the rth component of the attribute mode, and its squared value indicates the variation explained for that combination of components (Kroonenberg and Basford, 1989; van Eeuwijk and Kroonenberg, 1995).

The number of components for each mode needs to be simultaneously determined for all modes. Therefore, several solutions have to be inspected to come to an adequate description of a data set (Kroonenberg and Basford, 1989).

It is possible to portray the relationships between the genotypes and attributes for each component of the environment in a joint plot, a variant of Gabriel's (1971) biplot (Basford et al., 1996). The joint plot diagram was used to depict the component scores of genotypes and attributes associated with the environment modes. In these plots, genotypes are represented by points and attributes by vectors from the origin. Genotypes located near the origin have all their values close to the attribute means, given that the data are

Table 1
Mode component scores (with adequacy of fit) for four attributes of 10 sunflower hybrids over 21 environments in Argentina (genotype groups: (1) northern-adapted; (2) central-adapted; (3) broadly adapted hybrids)

Code	Name	Group[a] (two-mode)	Region[b]	Component scores			Proportion of SS explained (%)
				1	2	3	
Genotypes							
1	Contiflor 15	2		0.61	−0.04	0.18	59
2	Aguará	1		0.53	−0.63	−0.38	73
3	GV23105	1		−0.75	−0.01	0.05	62
4	GV25015	1		−0.73	−1.02	0.15	79
5	GV25086	3		0.26	0.40	−0.12	40
6	TC 2001	2		0.54	0.13	0.46	69
7	GV23146	3		0.41	0.16	−0.47	46
8	GV22510	3		0.04	0.18	−0.22	20
9	Contiflor 9	2		0.18	0.21	0.47	51
10	Morgan 734	1		−1.09	0.63	−0.12	81
Proportion of SS explained (%)				35	21	9	65
Environments							
9J7	9 de Julio	5	C	0.81	0.26	–	71
9J8	9 de Julio	6	C	0.81	0.06	–	67
9J9	9 de Julio	6	C	0.80	0.31	–	74
DX8	Daireaux	4	C	0.76	0.39	–	73
DX9	Daireaux	6	C	0.85	0.26	–	78
SA9	Sampacho	5	C	0.77	0.34	–	70
VT7	Venado Tuerto	4	C	0.78	0.28	–	69
VT8	Venado Tuerto	5	C	0.69	0.24	–	54
VT9	Venado Tuerto	5	C	0.77	0.35	–	71
V27	Venado Tuerto	1	M	0.57	−0.63	–	73
V29	Venado Tuerto	2	M	0.81	−0.23	–	71
VI9	Venado Tuerto	4	M	0.60	0.23	–	42
LB7	Las Breñas	1	N	0.34	−0.66	–	55
MA8	Margarita	3	N	0.62	−0.14	–	40
MA9	Margarita	6	N	0.83	−0.01	–	68
OR7	Orán	2	N	0.80	−0.51	–	89
OR9	Orán	2	N	0.73	−0.35	–	66
PA9	Paraná	1	N	0.70	−0.35	–	61
RE7	Reconquista	2	N	0.67	−0.33	–	56
RE8	Reconquista	3	N	0.63	−0.19	–	43
RE9	Reconquista	6	N	0.88	0.05	–	78
Proportion of SS explained (%)				54	11	–	65
Attributes							
OY	Oil yield (kg ha^{-1})			0.52	−0.42	0.23	50
GN	Grain number per square meter			0.51	0.37	0.32	51
GW	1000 grain weight (g)			−0.51	−0.68	0.18	76
OC	Oil content (%)			0.79	−0.41	−0.24	84
Proportion of SS explained (%)				35	24	6	65

[a] Groups in two-mode identified by hierarchical agglomerative clustering of oil yield (de la Vega et al., 2001).

[b] C: central region; N: northern region; M: managed environments.

Table 2
Mode component scores (with adequacy of fit) for three attributes of 10 sunflower hybrids over 11 environments in Argentina

Code	Name	Region[a]	Component scores				Proportion of SS explained (%)
			1	2	3	4	
Genotypes							
1	Contiflor 15		−0.42	0.12	−0.47	−0.09	74
2	Aguará		0.31	−0.39	−0.03	−0.44	57
3	GV23105		0.94	0.33	0.31	0.40	84
4	GV25015		0.35	−0.85	−0.48	0.20	74
5	GV25086		−0.26	0.19	0.36	0.41	46
6	TC 2001		−0.40	0.37	−0.49	−0.00	83
7	GV23146		−0.80	−0.59	0.37	0.14	81
8	GV22510		0.21	−0.09	0.64	−0.26	56
9	Contiflor 9		−0.33	0.61	0.02	−0.10	42
10	Morgan 734		0.40	0.29	0.04	−0.27	45
Proportion of SS explained (%)			24	20	14	7	65
Environments							
9J9	9 de Julio	C	0.81	−0.12	0.14	−0.08	70
DX9	Daireaux	C	0.87	−0.12	0.12	0.07	79
SA9	Sampacho	C	0.36	0.30	−0.40	−0.13	39
VT7	Venado Tuerto	C	0.35	0.51	−0.31	−0.37	61
VT9	Venado Tuerto	C	0.68	0.36	−0.02	0.09	60
V27	Venado Tuerto	M	−0.01	−0.49	−0.48	−0.19	50
V29	Venado Tuerto	M	0.02	−0.46	−0.28	0.45	49
VI9	Venado Tuerto	M	0.62	0.18	−0.57	0.26	81
MA9	Margarita	N	0.61	−0.55	0.37	−0.26	87
PA9	Paraná	N	−0.28	−0.67	−0.47	−0.25	80
RE9	Reconquista	N	0.47	−0.63	0.09	0.10	63
Proportion of SS explained (%)			29	19	12	6	65
Attributes							
CY	Oil-corrected yield (kg ha^{-1})		0.81	−0.07	–	–	66
BI	Total biomass (g m^{-2})		0.39	−0.67	–	–	61
HI	Harvest index		0.71	0.45	–	–	70
Proportion of SS explained (%)			44	22	–	–	65

[a] C: central region; N: northern region; M: managed environments.

attribute centered. Genotypes that are close together are similar in their specific responses for all attributes analyzed. For any particular attribute, genotypes can be compared by projecting a perpendicular from the genotype points to the attribute vector, i.e. entries that are further along in the positive direction of an attribute vector show higher values for this attribute and vice versa. The joint plots also display the strength of the associations among attributes. Acute angles between any two attribute vectors indicate positive associations, i.e. they are positively correlated, 90° angles indicate no association, and angles greater than 90° indicate negative associations (Chapman et al., 1997; Kroonenberg, 1997).

The three-mode principal component analysis was applied to the 10 × 21 × 4 and the 10 × 11 × 3 (G× E × A) matrices using the program TUCKALS3 (Kroonenberg, 1994). Prior to analysis, the data were standardized within environments according to the findings of Fox and Rosielle (1982) for two-mode analysis. Standardization of attributes (subtracting attribute mean and then dividing by the attribute standard deviation) within environments was necessary as attributes are recorded in different scales.

3. Results and discussion

3.1. Three-mode PCA of the components of oil yield

Several solutions with different numbers of components for each of the modes were tested. The three-mode model with 3 × 2 × 3 components for genotypes, environments, and attributes, respectively, was considered adequate for fitting the data ($r^2 = 0.65$), on the basis of informal judgments of the increases in r^2 compared to the increases in dimensions and difficulty of interpretation. In this model, the three components for the genotype mode accounted for 35, 21, and 9% of the variation, respectively; the two components for the environment mode accounted for 54 and 11%, respectively; and the three components for the attributes accounted for 35, 24, and 6% of the variation, respectively. Not all genotypes, environments, and attributes were fitted equally well by the model. For three of the 10 genotypes, the model accounted for less than 50% of the variability in their response compared to the overall fit of 65% (Table 1), namely entries 8 (20%), 5 (40%), and 7 (46%). In the two-mode clustering of oil yield (de la Vega et al., 2001), these three hybrids were the members of a genotype group that had a small interaction with environment (i.e. broadly adapted hybrids). Three northern-adapted hybrids, namely entries 10 (81%), 4 (79%), and 2 (73%) had the majority of their variance explained. Environments were generally well fitted by two components with more than 54% of the variation accounted for in most of them (Table 1), except for MA8 (40%), VI9 (42%), and RE8 (43%). MA8 and RE8 were the two lowest yielding northern environments, severely affected by rainfall excess during flowering and grain filling. They were grouped in a separate cluster by two-mode clustering of oil yield (de la Vega et al., 2001). Even though there were differences in fit among the attributes, the model accounted for more than 50% of the variation in all of them (Table 1).

3.1.1. Components description

Treating the components of the three modes separately gives only a partial view of the structure of the variability in the data, it being necessary to look at the components for all modes simultaneously for a full view (Kroonenberg and Basford, 1989). The components of the genotypes and those of the attributes (Table 1) do not have obvious interpretations with respect to mean trait values, although the lower-dimensional representations serve the purpose of data reduction. While the first environment component (54% of the variation) did not distinguish among environments (i.e. it explained the common pattern over environments), the second component (11% of the variation) contrasted central- and northern-type environments (Table 1). Thus, the joint plot of genotypes and attributes for the first environment component will be used to investigate the interactions between genotypes and attributes for all environments together and the joint plot of genotypes and attributes for the second environment component will be used to investigate the relative merit of each oil yield determinant underlying the observed G × E interactions.

3.1.2. First environment component: interpreting the attributes contributing to mean oil yield across environments

The standardized component weights for the first, the second, and the third axes of the joint plot of genotypes and attributes in the first environment component were 0.32, 0.20, and 0.01, respectively. The analysis of the joint plot of the first two axes (Fig. 1) showed that oil content was positively correlated to oil yield, since their vectors form an acute angle, while grain weight and grain number showed lack of association with oil yield as they are at right angles. To evaluate the importance of an attribute for each genotype, one has to compare the projections of each genotype on the attribute vector, i.e. the highest yielding genotypes across all environments tend to be on the bottom right quadrant of the joint plot. These hybrids were hence associated with better than average attribute scores for oil content. Entries 5 and 7, defined as broadly adapted hybrids by de la Vega et al. (2001), were the highest yielding genotypes across environments, while entry 4 was the lowest yielding hybrid. There is a strong negative association between grain weight and grain number, since their vectors form an almost 180° angle. The hybrids with the highest values for grain number are on the top right quadrant of the diagram, while the hybrids with the highest attribute scores for grain weight are on the bottom left quadrant. The highest yielding hybrids

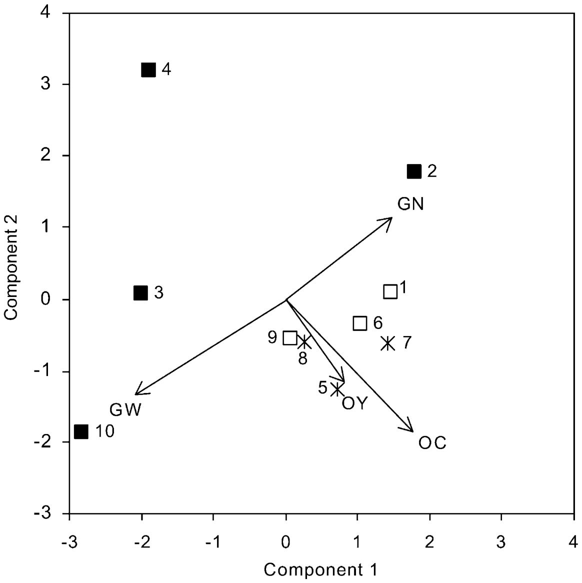

Fig. 1. Joint plot of the first two components of 10 sunflower hybrids and four attributes associated with the first environment component. Genotypes are represented by numbers (see Table 1 for genotype names). Genotype symbols represent groups identified by hierarchical agglomerative clustering of oil yield (de la Vega et al., 2001): northern-adapted hybrids (2, 3, 4, 10), central-adapted hybrids (1, 6, 9), and broadly adapted hybrids (5, 7, 8). Vectors for attributes: oil yield (OY), grain number (GN), grain weight (GW), and oil content (OC).

across environments had intermediate values for grain number and grain weight. The hybrids with the lowest average oil content across environments (entries 3, 4, and 10) have achenes with white-pigmented hypodermis. The dominant factor (*Hyp*) determining the presence of white-pigmented hypodermis is located in the same map interval as one quantitative trait locus with major effects on seed oil percentage (Leon et al., 1996).

More grains that are slightly lighter in weight and of greater oil concentration accounted for most of the variation in sunflower oil yield between open-pollinated cultivars and hybrids in Argentina between 1930 and 1995 (López Pereira et al., 1999). Within the set of hybrids evaluated in this study, oil content is the only yield determinant associated with oil yield. In part, this could be because the hybrids that showed the extreme values for grain number and grain weight, i.e. entries 2 and 10, respectively, showed a similar average performance for oil yield.

The strong negative association between grain number and grain weight found in this study suggests that further improvements in one of these attributes would be achieved at expense of the other and vice versa. López Pereira et al. (1999) also found a significant negative correlation between both traits. They suggest that future advances in sunflower breeding for yield potential should come from the breakage of the observed trade-off between these yield components. The standardized weight of the third axis of this joint plot is too small to warrant discussion.

3.1.3. Second environment component: contrasting central- and northern-type environments

Major differences between the central- and northern-type environments can be described in a single dimension, corresponding to the first component of the joint plot of genotypes and attributes for the second environment component (Fig. 2). This figure displays those aspects of the genotype and attribute relationships that are influenced by the differences between northern and central environments on genotypes and attributes, after the effect of average performance (Fig. 1) has been removed.

Central- and northern-type environments had positive and negative scores, respectively, for the component 1 of this joint plot. Mega-environment effects were very strong for oil yield, this attribute being the best indicator of the contrasting effects of the two types of environments. Regarding the oil yield determinants, mega-environment effects were stronger for grain number than for grain weight and oil content, indicating that this attribute accounted for most of the observed G × E interactions for oil yield. This could be in part because grain number in sunflower is determined between floral initiation and the start of rapid kernel growth (Connor and Hall, 1997), a longer period compared with the windows of determination of grain weight and oil content.

A product term to compare scores may be calculated as a product of any combination of the scores of the three modes given in Fig. 2, e.g. entry 6 (score 2.1) will have a positive product for oil yield (score 1.8) in a central environment as 9J9 (score 0.3). For the same environment type and attribute, entry 10 (score -1.5) would have a negative product. Entry 10 in a northern-type environment as LB7 (score -0.6) will have a positive product for oil yield and for the other

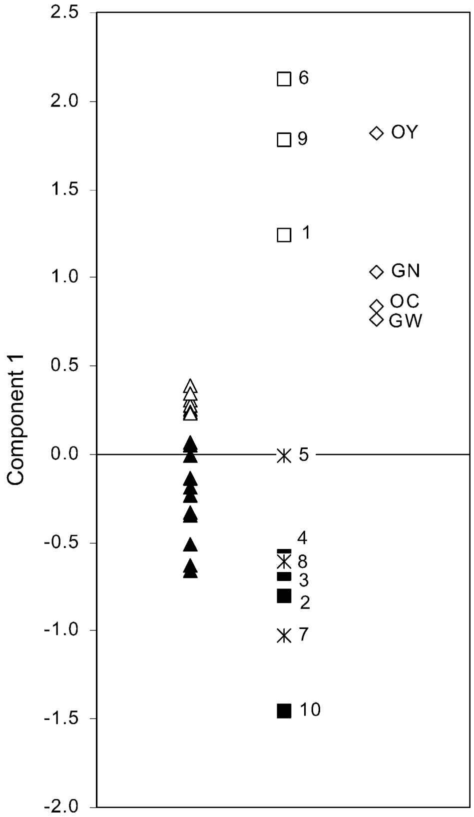

Fig. 2. First joint plot component for environments, genotypes, and attributes associated with the second environment component. Environment symbols represent: central-type environment (including VI9, open triangles) and northern-type environment (including V27 and V29, black triangles) (Table 2). Genotype symbols represent groups identified by hierarchical agglomerative clustering of oil yield (de la Vega et al., 2001): northern-adapted hybrids (2, 3, 4, 10), central-adapted hybrids (1, 6, 9), and broadly adapted hybrids (5, 7, 8). Attributes: oil yield (OY), grain number (GN), grain weight (GW), and oil content (OC).

attributes, considering that all of them had positive scores. As oil yield is the attribute that showed the highest score, the magnitude of its G × E × A products will be larger than the product terms of its determinants. The distinction between the environment types seems primarily due to the northern and central specifically adapted genotype groups, rather than the broadly adapted hybrids, located relatively close to the origin (Fig. 2). December plantings in Venado Tuerto under natural photoperiods associated with northern environments in this joint plot, while December planting in Venado Tuerto with artificially extended photoperiod associated with the central environments.

3.2. Three-mode PCA of the determinants of oil-corrected grain yield

The three-mode model with 4 × 4 × 3 components for genotypes, environments, and attributes, respectively, was considered adequate for fitting the data ($r^2 = 0.65$) after testing several other combinations of numbers of components for each mode. In this model, the four components for the genotype mode accounted for 24, 20, 14, and 7% of the variation, respectively; the four components for the environment mode accounted for 29, 19, 12, and 6%, respectively; and the two components for the attribute mode accounted for 44 and 22% of the variation, respectively. For three of the 10 genotypes, the model accounted for less than 56% of the variability in their response compared to the overall fit of 65% (Table 2), namely entries 9 (42%), 10 (45%), and 5 (46%). Environments were generally well fitted by four components (Table 2), except for SA9 (39%). The model accounted for more than 61% of the variation in all attributes (Table 2).

3.2.1. Components description

The components of the genotypes and those of the attributes (Table 2) do not have obvious interpretations, and the lower-dimensional representations serve the purpose of data reduction. The first environment component (29% of the variation) explained the common pattern over environments. The second component (19% of the variation) contrasted central- and northern-type environments (Table 2). The joint plot of genotypes and attributes for the first environment component will be used to investigate the interactions between genotypes and attributes across environments and the joint plot of genotypes and attributes for the second environment component will be used to investigate the relative merit of each determinant of oil-corrected grain yield in underlying the observed G × E interactions.

3.2.2. First environment component: attributes contributing to mean oil-corrected grain yield across environments

The standardized component weights for the first and the second axes of the join plot of genotypes and

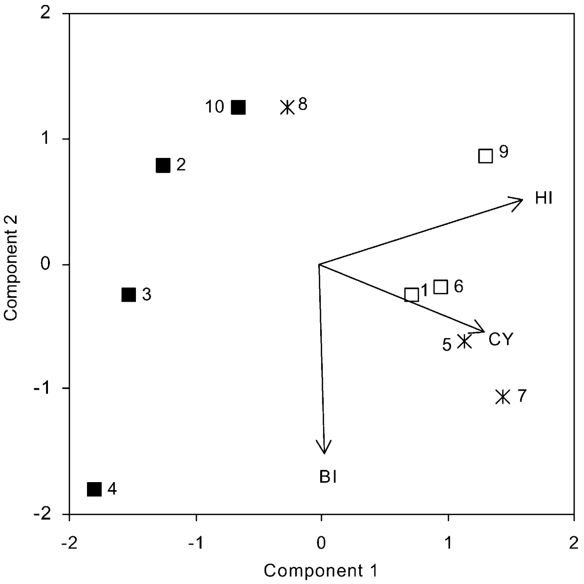

Fig. 3. Joint plot of the first two components of 10 sunflower hybrids and three attributes associated with the first environment component. Genotypes are represented by numbers (see Table 1 for genotype names). Genotype symbols represent groups identified by hierarchical agglomerative clustering of oil yield (de la Vega et al., 2001): northern-adapted hybrids (2, 3, 4, 10), central-adapted hybrids (1, 6, 9), and broadly adapted hybrids (5, 7, 8). Vectors for attributes: oil-corrected grain yield (CY), total oil-corrected biomass (BI), and harvest index (HI).

attributes in the first environment component were 0.20 and 0.09, respectively. The analysis of the joint plot of these two axes (Fig. 3) showed that oil-corrected biomass and harvest index were both positively correlated to oil-corrected yield (i.e. their attribute vectors form acute angles). The correlation between oil-corrected yield and harvest index was slightly larger, indicating that harvest index accounted for a larger portion of the variation of mean oil-corrected yield. These observations agreed with those previously made in sunflower (Fereres et al., 1986; Sadras and Villalobos, 1994) and in other crops (e.g. Chandler, 1969; Meredith and Wells, 1989; Slafer et al., 1994), where it was found that yield increases through selection have been primarily through changes in partitioning dry matter from vegetative to reproductive structures rather than improvements in biomass production. The comparison between the harvest index of current sunflower hybrids and those achieved in other crops (e.g. Andrade, 1995) suggests that, at least in the near future, yield increases through partitioning from vegetative to reproductive structures is likely to continue. Sadras and Villalobos (1994) highlighted that longer grain-filling period would be a trait with great influence on harvest index and yield, and more work is necessary to identify genotypic variability for this trait and to establish the practical possibilities of breeding and selection. The highest yielding genotypes across all environments tend to be on the bottom right-corner of the joint plot. These hybrids were hence associated with better than average attribute scores for both oil-corrected biomass and harvest index. The highest yielding hybrid across environments (entry 7) showed the second largest value for both traits (Fig. 3).

The angle between the attribute vectors of oil-corrected biomass and harvest index was slightly larger than 90°, which indicates that these attributes had a weak negative association. Entry 4, for example, showed the highest value for oil-corrected biomass and the lowest harvest index within the reference set of genotypes used in this study (Fig. 3). The hybrids with the highest values for harvest index are on the right-hand side of the diagram, while the hybrids with the highest attribute scores for oil-corrected are on the bottom part of the joint plot. Further advances in yield potential could be achieved through simultaneous improvements for both traits, which should bring successive advances toward the bottom right-corner of the joint plot.

3.2.3. Second environment component: contrasting central- and northern-type environments

As was the case for yield components, major differences between the central- and northern-type environments in discriminating among genotypes and attributes are described in a single dimension, corresponding to the first component of the joint plot of genotypes and attributes for the second environment component (Fig. 4).

Central- and northern-type environments had positive and negative scores, respectively, for the component 1 of this joint plot, except for the central environments DA9 and 9J9 (scores −0.12). In this reduced set of environments, hybrids 3 and 10 (northern-adapted hybrids) showed positive product terms in the central-type environments. Mega-environment effects were strong for oil-corrected yield and oil-corrected biomass, indicating that, conversely to the

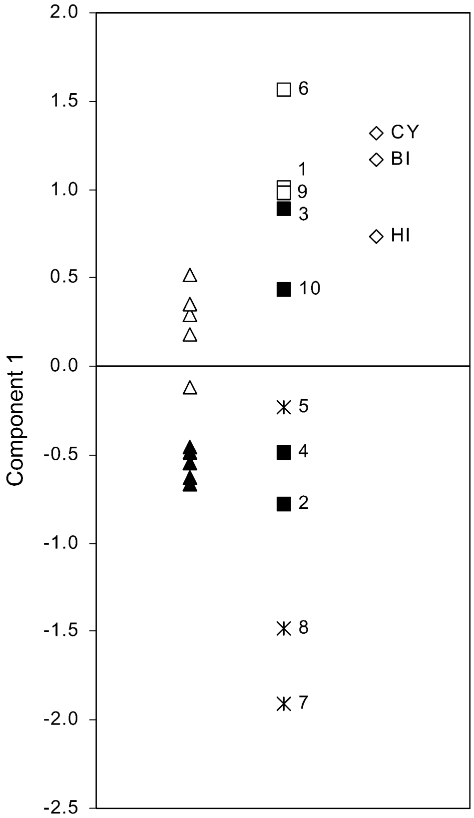

Fig. 4. First joint plot component for environments, genotypes, and attributes associated with the second environment component. Environment symbols represent: central-type environment (open triangles) and northern-type environment (black triangles). Genotype symbols represent groups identified by hierarchical agglomerative clustering of oil yield (de la Vega et al., 2001): northern-adapted hybrids (2, 3, 4, 10), central-adapted hybrids (1, 6, 9), and broadly adapted hybrids (5, 7, 8). Attributes: oil-corrected grain yield (CY), total oil-corrected biomass (BI), and harvest index (HI).

determination of mean yield, oil-corrected biomass accounted for most of the observed G × E interactions for oil-corrected yield. This suggest that further advances in selection for specific adaptation to the northern and the central mega-environments separately could be achieved through improvements in total dry matter production within each environment type. The distinction between the environment types seems primarily due to the central and broadly adapted genotype groups, rather than the northern-adapted hybrids, located relatively closer to the origin (Fig. 4).

4. Conclusions

While the record shows that agronomic and breeding advance can be achieved empirically through "trial and error", more rapid progress can be aided when some understanding of the physiological bases of crop performance is established and selection criteria is defined in terms of specific traits (Lawn and Imrie, 1991). Yield component traits have been the subject of numerous physiological and genetical analyses, but the results of these studies are often equivocal and of limited value as guides to plant breeders. This may be in part because of compensation, that can be genetically determined and also be a consequence of environmental conditions (Austin, 1993).

Where independent two-way analyses are attempted for different attributes in a G × E system, it is very difficult to assess jointly information on multiple attributes integrated across environments, because one mode disappears from the analysis. The response plots and biplots shown in de la Vega et al. (2001) suggested that all yield components and determinants are involved in the genotype-specific responses for yield, i.e. all of them differentiated between central and northern environments. They also suggested the existence of different specific responses in terms of physiological determinants and components of yield to specific environmental challenges within the same genotype groups. Combining the individual two-way analyses for their joint interpretation would result in a very subjective appreciation of the relative merit of each attribute in determining the G and G × E interaction effects on yield. Three-mode principal component analysis may clarify structures that are inaccessible via two-way methods (van Eeuwijk and Kroonenberg, 1995) by describing the underlying complex situation in a low-dimensional space (Kroonenberg and Basford, 1989). Joint plots, for example, provide a powerful graphic to assist in this process (Basford et al., 1996) and have helped to enhance the interpretation of the influence of yield determinants on the G and G × E interaction effects for yield in sunflower within this multi-environment trial. Different yield determinants accounted for most of the variation in genotype average performance (i.e. yield potential and broad adaptation) and specific response patterns of genotypes across environments (i.e. specific adaptation) within each of the two analytical frameworks used. Oil content and harvest index variations were strongly associated with variations in mean oil yield across environments. Grain number and total oil-corrected biomass yield were the main underlying determinants of the contrasting genotypic performance between central and northern environment-types.

Future sunflower breeding avenues for yield potential should target the trade-off between grain number and grain weight. Specific adaptation to both environment types could be addressed by selecting for larger relative grain number and oil-corrected aboveground biomass yield in particular environments.

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