PHYSIOLOGICAL BASES OF GENOTYPE BY ENVIRONMENT INTERACTIONS FOR SOWING DATE IN SUNFLOWER

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Summary

Crop yield in a given environment can be explained in terms of intercepted radiation (IR), radiation use efficiency (RUE), harvest index (HI) and grain oil content (%). Within this physiological framework, the objective of this paper is to analyze the observed genotype by environment (G×E) interaction for sunflower between central (C) and northern (N) growing regions of Argentina in terms of the responses of the indicated variables and other morpho-physiological attributes. The overall objective is to identify putative indicators of adaptation to N environments.

A reference set of genotypes were grown at Venado Tuerto using October (C-environment) and December (a managed-environment previously shown to be a good surrogate for the N region) planting dates. A significant G×E interaction was found for almost all measured traits. The changes in the hybrid relative performance among environments were associated with all yield components. Differences in grain number were associated with failures in seed set in the central sector of the head rather than to differences in the number of flowers. These changes were not related to differences in IR at anthesis. Changes in rate and duration of grain filling were associated with IR and RUE during flowering to physiological maturity, and determined differences in grain weight, oil content and HI. It is concluded that if the December planting date in Venado Tuerto is used as indirect selection environment for the N region, head center seed set and stay green during grain filling serve as putative indicators of adaptation.

Introduction

In Argentina, sunflower is grown over a large geographical area that includes temperate and subtropical environments. Within this range of environments, genotype by environment (G×E) interactions complicate selection and breeding strategies. These interactions reflect differences in genotype adaptation, which may be exploited by selection for broad or specific adaptation. Pattern analysis of a reference set of sunflower hybrids grown over 21 northern (N), central (C) and managed (M) environments of Argentina (de la Vega *et al*., 2000) has shown that: (1) the effects of N and C environments on genotype discrimination indicate the existence of two mega-environments, and the possibility of selecting for specific adaptation; (2) December planting dates in a C location (Venado Tuerto) were positively correlated with the N environments, representing an opportunity for indirect selection; (3) some hybrids of contrasting response patterns in terms of yield components, showed similar patterns of relative performance for oil yield, suggesting the existence of different specific genotypic responses to specific environmental challenges within the same groups. Better knowledge of the physiological basis of the genotypic performance in variable environments should increase the speed at which superior genotypes are identified/developed. A useful framework to investigate and understand environmental effects on yield defines crop yield as the product of the intercepted radiation (IR), the efficiency of the crop in converting radiation into dry matter (RUE) and the fraction of that biomass partitioned to harvestable yield (HI) (Charles-Edwards *et al.*, 1982). Within this physiological framework, the objective of this study is to analyze the observed G×E interaction for sunflower between October and December planting dates in Venado Tuerto in terms of the responses of the indicated variables and other morpho-physiological attributes. The overall objective is to identify putative indicators of adaptation to N environments that contribute to increase the efficiency of indirect selection.

Materials and Methods

Crops of a reference set of 10 sunflower hybrids (Table 1) were grown at Venado Tuerto using October (S1, C-environment) and December (S2, a managed-environment previously shown to be a good surrogate for the N region) planting dates during 1996/97 (Experiment 1) and 1998/99 (Experiment 2) seasons. Planting date and genotype constituted main-plot and sub-plot of split-plot trials with 3 reps. Planting dates were: Experiment 1: S1: 28/10/96, S2: 14/12/96; Experiment 2: S1: 22/10/98, S2: 19/12/98. Leaf area index (LAI) was estimated weekly. The proportion of the incident radiation intercepted by the crop (*Q*d) was estimated from LAI measurements. The dynamics of above-ground dry matter accumulation, individual grain weight and HI were followed as described in de la Vega and Hall (2000). Data of number of flowers m^{-2}, empty center diameter, grain weight, oil content, grain yield and oil yield were recorded. RUE was estimated as the slope of the function that describes oil-corrected biomass/cumulative IR relationships.

ANOVA was conducted within each experiment to examine the partitioning of sums of squares to G, E and G×E interaction for each attribute. Principal component analysis (PCA) was applied to the matrices of genotypes and environments for the response indices of each attribute for both experiments. Response indices were calculated by dividing the value of each attribute in S2 by its value in S1. The principal components (PCs) of the squared Euclidean distance matrices were estimated using a singular value decomposition procedure (Gabriel, 1971). Treatment 4 was excluded from PCA because it was severely damaged by storms in S2 1998/99.

Results

Mean oil yield was significantly higher in S1 in both experiments ($P < 0.001$), as its components grain yield ($P < 0.001$) and oil content ($P < 0.001$). A significant G×E interaction was found for oil yield in both experiments ($P < 0.01$) and for almost all measured traits (Table 1). The changes in the hybrid relative performance among environments were associated with grain number, grain weight and oil content. The results of the PCAs of the matrices of genotype-attribute response indices are presented in biplots of the 1st and 2nd PCs (Figure 1). Entries that are close together are similar in response patterns of all attributes analyzed across testing environments. For any particular attribute response index, genotypes can be compared by projecting a perpendicular from the genotype markers to the response index vector, i.e. entries that are further along in the positive direction of the vector show higher response indices for this attribute and vice versa (Kroonenberg, 1997). Acute angles between any two vectors of response index indicate positive associations, i.e. they influence the genotypic relative performance for a particular attribute in a similar manner; 90º angles indicate no association; and angles greater than 90º indicate negative associations.

In spite of the variations due to the G×Y interaction, both experiments showed strong coincidences in genotype discrimination and attribute association. The 1st PC showed a strong positive association with the vector of the response index for oil yield in both experiments, with the hybrids that performed better in S2 relative to S1 located on the right half of the diagrams and vice versa. In Experiment 2, the vector of oil yield showed also a positive association with the 2nd PC, and then, the hybrids that performed better in S2 relative to S1 tended to be located on the top right quadrant of the biplot. The 2nd PC appears to account for the contrasting responses of the hybrids adapted to S2 in terms of yield-related attributes.

For both experiments, treatments 1, 6 and 9 (C-adapted hybrids [de la Vega *et al*., 2000]) showed the lowest values of response index for oil yield, which indicates that they would not be well adapted to S2. Treatments 5 and 8 (broadly-adapted hybrids) were located near to the origin, indicating that they showed response indices close to the average for all attributes analyzed. Treatments 3 and 10 (N-adapted hybrids), showed high values of response index for oil yield, associated to high response indices for oil content, kernel percentage, IR between flowering and physiological maturity (F-PM), HI, rate of daily HI increase and grain filling duration. Treatments 2 and 7 (N-adapted and broadly-adapted hybrids, respectively), showed a high oil yield in S2 relative to S1, associated to high response indices for grain yield, grain weight, total biomass yield, grain filling rate and RUE in F-PM. The vector of the response index of oil yield showed a negative association with the diameter of the empty center of the head in both experiments. Grain filling duration exhibited strong positive associations with IR in F-PM, oil content, kernel percentage, HI, and rate of linear HI increase. Grain filling rate showed positive associations with grain weight, RUE in F-PM, and total biomass yield.

Discussion

The environments analyzed in this paper showed strong discrimination effects on the patterns of relative performance of the reference genotypes. The changes in the hybrid relative performance among environments were associated with all components of oil yield. Differences in grain number were associated with failures in seed set in the central sector of the head rather than to differences in the number of developed flowers. These changes were not related to differences in IR at anthesis. Changes in rate and duration of grain filling were associated with IR and RUE during flowering to physiological maturity, and determined differences in grain weight, oil content and HI. Lower oil content in S2 was not related to a

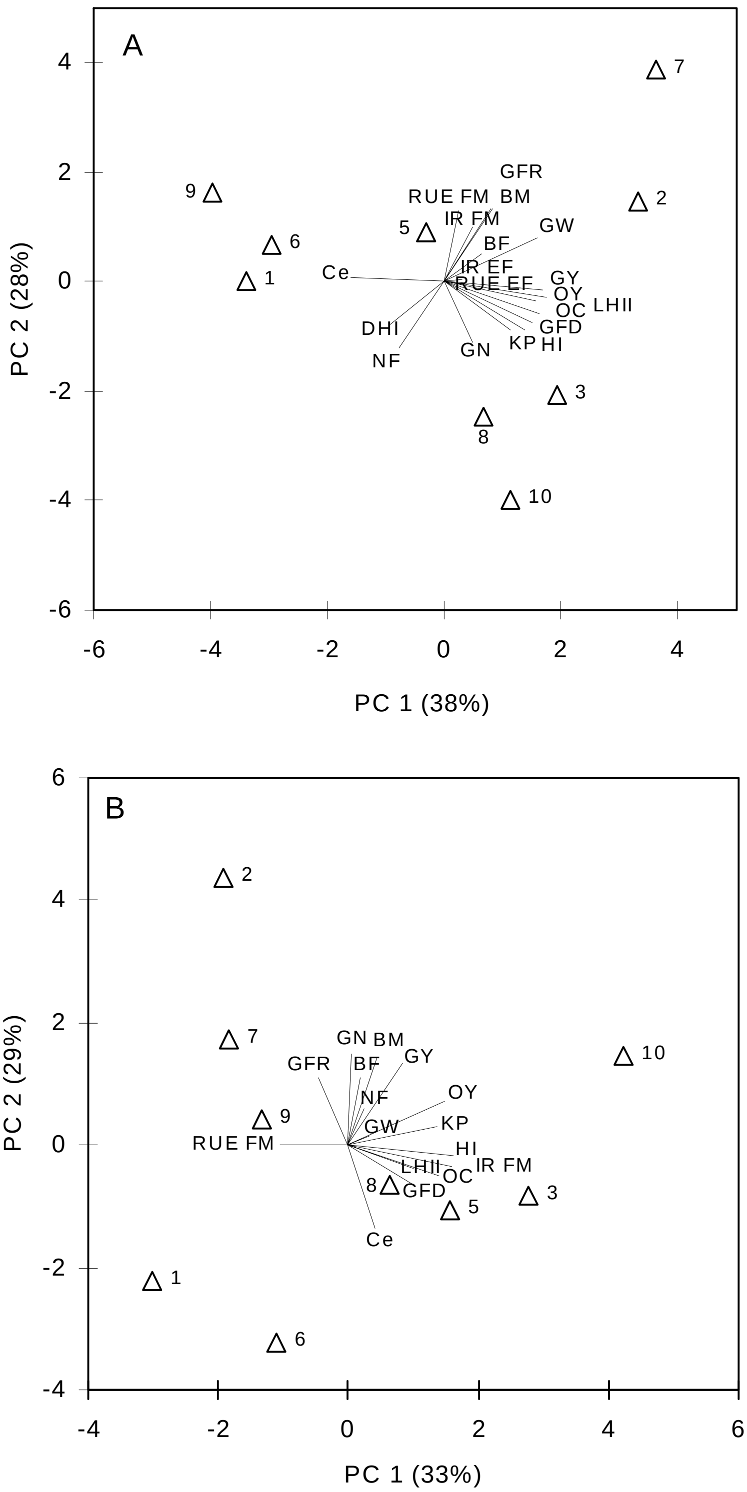

Figure 1. Biplot of the 1st and the 2nd principal components of 9 sunflower hybrids and the response indices of 19 (A) and 16 (B) morpho-physiological attributes in December vs. October planting dates in Venado Tuerto 1996/97 (A) and 1998/99 (B). Attributes are: oil yield (OY), grain yield (GY), oil content (OC), diameter of the empty center (Ce), number of flowers (NF), grain number (GN), grain filling rate (GFR), grain weight (GW), grain filling duration (GFD), kernel percentage (KP), intercepted radiation from emergency to flowering (IR EF), intercepted radiation from flowering to maturity (IR FM), radiation use efficiency from emergency to flowering (RUE EF), radiation use efficiency from flowering to maturity (RUE FM), total biomass at flowering (BF), total biomass at maturity (BM), harvest index (HI), daily linear HI increase (LHII), linear HI increase duration (DHI) (See Table 1 for hybrid codes)

Table 1. Mean values of yield and growth components for 10 sunflower genotypes grown in Venado Tuerto 1996/97 and 1998/99 under October (S1) and December (S2) planting dates. IR: intercepted radiation; RUE: radiation use efficiency; HI: harvest index; E: emergency; F: flowering; PM: physiological maturity

	Genotype	Oil yield (kg ha^{-1})		Number of flowers m^{-2}		Grain number m^{-2}		Empty center (cm)		Grain weight (mg achene^{-1})		Oil (%)		IR E-F (MJ m^{-2})		IR F-PM (MJ m^{-2})		RUE E-F (g MJ^{-1} m^{-2})		RUE F-PM (g MJ^{-1} m^{-2})		Corrected biomass yield (g m^{-2})		HI	
		S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
Experiment 1 (1996/97)																									
1	Contiflor 15	1697	821	8297	9296	6612	6340	0.60	4.37	42.6	27.6	51.6	38.4	718	635	698	396	1.52	1.71	1.10	0.82	1673	1267	0.37	0.28
2	Aguará	1418	1241	10306	9880	8201	8135	0.00	0.53	29.2	34.1	46.2	40.5	764	717	682	465	1.48	1.48	0.78	0.88	1554	1387	0.36	0.35
3	GV23105	1537	1249	7628	9481	5723	6060	2.57	5.40	52.2	47.7	45.3	41.0	658	624	671	484	1.79	1.66	1.06	1.36	2116	1693	0.34	0.40
4	GV25015	1473	1106	9428	8927	8509	6115	0.50	0.87	33.6	44.2	39.5	36.2	758	728	625	424	1.53	1.34	0.72	1.16	1540	1588	0.34	0.36
5	GV25086	1992	1175	7871	8353	6253	5286	0.37	2.57	55.0	45.7	52.5	44.6	614	540	695	475	1.64	1.63	1.18	1.28	1786	1398	0.40	0.39
6	TC 2001	1722	744	8486	9061	6754	5030	0.87	4.73	40.9	28.5	52.2	39.8	728	639	667	405	1.50	1.41	1.13	0.73	1673	1283	0.37	0.30
7	GV23146	1534	1296	9159	7931	8119	5514	0.80	1.40	30.5	41.8	48.6	44.8	736	674	648	444	1.52	1.5	0.60	1.47	1492	1466	0.37	0.35
8	GV22510	1498	1310	8475	9208	5266	6396	0.80	4.83	54.4	39.9	48.9	45.1	682	626	724	486	1.41	1.47	1.09	0.48	1620	1207	0.35	0.38
9	Contiflor 9	1724	602	7710	9079	5928	4266	0.63	4.83	48.2	28.5	51.3	38.1	659	586	687	413	1.75	1.36	0.98	1.59	1919	1520	0.41	0.32
10	Morgan 734	1494	1041	4723	5836	4266	3947	0.00	1.13	71.4	52.9	44.7	42.4	643	537	642	487	1.79	1.58	1.09	0.87	1975	1221	0.34	0.36
	Media	1609	1058	8208	8705	6563	5709	0.71	3.07	45.8	39.1	48.1	41.1	696	631	674	448	1.59	1.51	0.97	1.06	1735	1403	0.37	0.35
		P	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.	*P*	l.s.d.
	G×S	***	258	NS	1364	**	1365	***	1.23	***	6.5	***	1.8	NS	35	*	55	NS	0.44	NS	0.99	NS	391	***	0.05
Experiment 2 (1998/99)																									
1	Contiflor 15	2228	930	9190	9214	7255	5153	0.00	3.21	56.6	33.9	51.9	44.6	-	-	719	392	-	-	2.21	0.87	2195	980	0.40	0.32
2	Aguará	1956	976	9674	9582	6614	7304	0.00	0.00	57.6	42.3	49.7	36.5	-	-	735	388	-	-	1.67	0.35	2266	1611	0.41	0.34
3	GV23105	1945	1096	8540	8948	6250	4933	0.00	5.63	66.7	53.3	44.5	41.6	-	-	608	398	-	-	2.03	0.51	2200	1299	0.37	0.37
4	GV25015	1665	623	12346	10006	7164	5587	1.38	5.13	56.8	41.1	39.3	27.6	-	-	555	335	-	-	1.55	1.60	2209	977	0.31	0.27
5	GV25086	1976	988	7917	9561	5987	5128	0.00	4.31	64.5	41.2	52.0	44.7	-	-	716	444	-	-	1.51	0.35	1985	1099	0.39	0.37
6	TC 2001	2338	890	9884	7869	7010	5206	0.00	5.79	47.6	36.4	52.1	43.2	-	-	671	393	-	-	1.68	1.31	2419	1250	0.39	0.35
7	GV23146	2217	1045	7343	8723	6665	6076	0.00	0.00	57.5	41.3	50.6	40.6	-	-	679	370	-	-	0.99	0.73	1730	1013	0.36	0.31
8	GV22510	1751	891	8646	8466	5303	4932	0.00	4.09	68.7	36.5	48.4	41.9	-	-	723	405	-	-	1.38	0.99	2016	1177	0.36	0.36
9	Contiflor 9	2067	908	7477	9014	5533	4943	0.00	3.38	73.8	37.2	50.9	43.2	-	-	740	393	-	-	1.55	0.37	1776	1060	0.39	0.34
10	Morgan 734	1773	1152	5927	6374	4806	4427	0.00	1.59	89.1	60.4	44.2	43.9	-	-	682	455	-	-	1.52	0.56	1879	1173	0.37	0.38
	Media	1992	950	8695	8778	6259	5369	0.15	3.31	63.9	42.4	48.4	40.8	-	-	683	397	-	-	1.61	0.72	2067	1164	0.37	0.34
		P	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.	*P*	d.m.s.
	G×S	**	269	NS	2030	**	950	***	1.90	**	8.8	***	1.4	-	-	***	47	-	-	NS	1.01	NS	310	NS	0.05

d.m.s. *P* = 0.05; ****P* < 0.001; ***P* < 0.01; **P* < 0.05

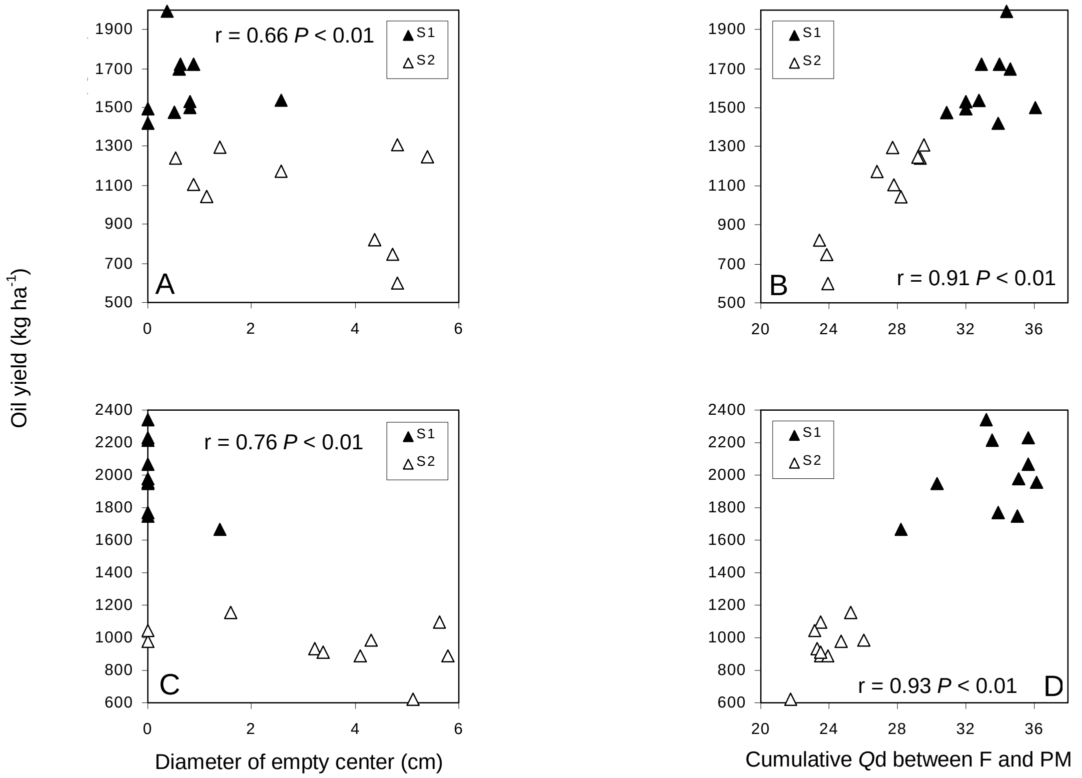

Figure 2. Empty head diameter/oil yield relationship in 1996/97 (A) and 1998/99 (C) and cumulative proportion of the incident radiation intercepted by the crop (*Q*d) between flowering (F) and physiological maturity (PM)/oil yield relationship in 1996/97 (B) and 1998/99 (D) for October (S1) and December (S2) planting dates at Venado Tuerto

lower kernel percentage. Austin (1993) highlighted that to be of value in assessing a trait in a population of plants, a screening test must satisfy a number of criteria, as follows: there must be heritable variation in the character; it should be possible to assess the character simply, rapidly and inexpensively; and there must be an appreciable genetic correlation between the attribute and yield under field conditions. It is concluded that if the December planting date in Venado Tuerto is used as indirect selection environment for the N region, head center seed set and stay green during grain filling serve as putative indicators of adaptation (Figure 2).

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