Selection response for oil content and agronomic performance in four subtropical maize populations

Alejandro Ortega-Corona#, Raymundo Picón-Rico[1], Ricardo E Preciado-Ortiz[1]*, Arturo D Terrón-Ibarra[1], Manuel de Jesús Guerrero-Herrera[2], Silverio García-Lara[3], Sergio O Serna-Saldivar[3]

[1]Bajio Experimental Station, Km 6.5 Carr Celaya–San Miguel Allende, 38010, Celaya, México
[2]Norman Borlaug Experimental Station, Km 12 Car. Dr Norman Borlaug, 85270 Cd Obregón, México
[3]Instituto Tecnológico de Estudios Superiores de Monterrey, Departamento de Biotecnología e Ingeniería de Alimentos, ITESM, CP 64849 Monterrey, México
*Corresponding author: E-mail: preciado.ernesto@inifap.gob.mx
#This paper is dedicated to the memory of Alejandro Ortega-Corona Ph.D., leader of the project to increase the oil content through recurrent selection in the four subtropical populations described in this paper.

Abstract

High oil content (HOC) maize (*Zea mays* L) genotypes may have an economic impact on animal husbandry and on food and feed industries in several countries due to their related high digestible energy value. Almost all knowledge about cultivating oil accumulation in maize kernels, using recurrent selection, have been generated in temperate regions, but very little is known about the genotypes commonly grown in subtropical regions. With the intention of developing the HOC in a subtropical maize germplasm in Celaya Mexico in 2004, a half-sib recurrent selection scheme was initiated using near infrared spectrophotometry in four Bajio and Northwest varieties of white and yellow kernel populations (BWP, NWP, BYP, and NYP). With the aim to study the selection response for oil content, grain yield and other traits, field experiments conducted during 2011 in Morelia, and during 2011 and 2012 in Celaya. Results by location and combined across locations showed no significant changes within populations in terms of grain yield and other agronomic characteristics, which is in contrast to the literature (grain yield has been show to decline as oil content increased). This response is due to the employed field selection criteria, which emphasized selecting healthy, top-yielding and agronomically superior individuals from each population. Regarding the oil content, a gradual increase over several cycles was obtained in the selected populations, using a selection gain per cycle of 0.31%, 0.40%, 0.27%, and 0.30% for BYP, NYP, BWP, and NWP, respectively. These improved populations contained final oil contents of 7.5%, 8.1%, 7.6%, and 6.7%, for BYP, NYP, BW, P, and NWP, respectively.

Keywords: Zea mays L, high oil content, selection response, recurrent selection, subtropical maize

Introduction

In several countries specialty maize hybrids have become more important due to increasing consumption by humans and livestock, as well as raw materials for value-added industries. Particularly, high oil maize genotypes have a high energetic value because caloric of oil contains 2.25 times more accumulated energy than both starch and protein, (Alexander, 1988). High oil maize is a desirable trait that can be selected to meet the high energy requirements in the feed for poultry, swine and dairy cattle (Misevic and Alexander, 1989).

Recurrent selection is a cyclical procedure designed to accumulate desirable traits in populations under selection. This is possible through a gradual increase in the frequency of favorable alleles for primary traits in the target environments of the breeding program (Hallauer, 2007). According to Hallauer and Miranda (1981), heritability for high oil content is approximately 70%, so a selection response is feasible. Selection for increased oil content through recurrent selection in maize, has been studied by several researchers: Dudley and Lambert (1992); Misevic and Alexander (1989); Song and Chen (2004); Hong-Wu et al (2009). Undoubtedly the most classic study was of high maize oil and protein breeding initiated at the University of Illinois by CG Hopkins in 1896. This effort improved the oil content from 4.5% to 22% (Dudley and Lambert, 2004). By 2005, 106 generations of selection for high oil content had been completed but the limits of selection had not yet been reached (Dudley, 2007). Unfortunately, almost all knowledge about oil accumulation in maize kernels through recurrent selection have been generated in temperate regions, so little is known about genotypes adapted to subtropical regions.

Currently selection for increased oil content has become relatively easy using nuclear magnetic resonance (NMR) and kernel analyzers (NIRA or near infrared analyzers) that use the reflection or transmission of near infrared rays, which effectively determine the oil, protein and starch contents. The major advan-

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tages of these non-destructive analytical techniques which employ whole kernels are quickness, precision and low cost (Alexander, 1988).

Nevertheless, the means of different populations selected for high oil content (HOC) through selection cycles, indicates barriers to increasing the oil and protein concentrations without reducing the starch concentration in the kernel (Dudley, 2007). Dudley and Lambert (1992) reported that for each point of increased oil percentage, the starch content was declined between 1.3% and 1.6%. Likewise Song and Chen (2004) reported that with each 1% increase in oil, the amount of assayable total starch decreased between 1.48% and 1.83%.

This negative correlation may be a result of reduced grain yield according to Alexander and Seif (1963); Dudley et al (1974; 1977); and Misevic and Alexander (1989). Rosulj et al (2002), reported reduced yields per cycle of 1.41% and 1.24% in the selected populations DS7u and YuSSSu, respectively. Pamin et al (1986), who observed positive genetic correlations between the oil content and grain yield in full sib progenies, reported the opposite response. Furthermore, selection of high oil content has been shown to induce higher grain moisture than cultivars with only 5% oil (Miller et al, 1981).

In a previous publication by this research team (Preciado-Ortiz et al, 2013), part of the data set in this paper was presented to emphasize the effects of recurrent selection on physical kernel properties, fatty acid profiles and lipophilic antioxidant capacities. The aim of this subsequent research is to analyze the recurrent selection process and the selection response from a plant breeding perspective.

More specifically, the cyclical response of recurrent selection for oil content, grain yield and other agronomic characteristics was researched in four subtropical maize populations grown in the Bajio area of Mexico.

Materials and Methods

Genetic materials

The four subtropical populations under recurrent selection to increase oil content were formed with a germplasm adapted to the Bajio and Northwest regions of Mexico, including two white or yellow kernel populations for each region. A brief description of the genetic background and adaptation of each population is as follows:

Bajio White Population (BWP): a broad genetic base population, formed by recombining a white subtropical germplasm, which includes breeding and experimental lines of the INIFAP's Bajio Maize Breeding Program, and landraces adapted to the Bajio region; the variety exhibited dent and semi dent grain texture with an initial oil content of 4.4 %.

Bajio Yellow Population (BYP): a broad-based population formed from a subtropical yellow germplasm adapted to the Bajio region; this variety formed through several cycles of recombination using breeding materials from the INIFAP's Bajio Maize Breeding Program, Germplasm Bank landraces, CIMMYT populations, and some advanced generations of hybrids; it exhibits a dent grain texture with an initial oil content of 4.5%.

Northwest White Population (NWP): this population was developed through the integration of an elite white germplasm adapted to the Northwest region of Mexico; it has a resistance to Puccinia polysora, excellent stalk quality, and a grain texture between flint to semi dent, with an initial oil content of 4.1%.

Northwest Yellow Population (NYP): formed from germplasm adapted to the Northwest region of Mexico, with tolerance to P. polysora and micoplasmosis; intense yellow-orange kernels, with flint texture; and an initial oil content of 4.5%.

The reason for simultaneously conducting recurrent selection in four populations from different genetic backgrounds and adaptations, was to concurrently improve opposite heterotic groups in the two white kernel (NWP and BWP) and the two yellow kernel (NYP and BYP) populations with the aim of developing high-yield hybrids with high oil content.

The Half Sib Recurrent Selection scheme, used to develop the four HOC subtropical populations, was previously documented by Preciado-Ortiz et al (2013). Briefly, each cycle of selection for each maize population was conducted in isolated plots established with 50 half sib HOC families, from the previous cycle. Each family was planted in a 5 m row as a female parent (detasseled); the male parent (pollinator) was a bulk composite of seeds with HOC, from each of the 50 families. The males were planted every other row (two females and one male). At harvest, 200 ears were selected from the best four plants in each family. As the selection criteria, a special emphasis was made on selecting the better plants with full competence, healthy and larger ears, medium plants and ear heights and those with no evidence of lodging or rotten stalks.

Selection for high oil content was performed in the laboratory with a NIR magnetic resonance equipment. The seeds of each of the 200 ears were screened with an INFRATEC 1241 (Tecator AB) with the aim of identifying the best 50 HOC families. Further selection of HOC individual seeds from within the best 50 HOC families was subsequently performed with an INFRATEC 1255 (Tecator AB), which selected 100 HOC seeds that were used to initiate a new cycle of selection in each of the four populations. The genetic material used to evaluate the progress of selection for oil content and agronomic performance came from the seeds of the male composites in each cycle (1 to 7 for BWP and BYP, and 1 to 8 for NWP and NYP).

Field Evaluation

This research consisted of two steps: a) cycles of recurrent selection initiated in 2004 at INIFAP's Bajio

Experimental Station in Celaya, Mexico on isolated selection plots for each population using the process described above; and b) the evaluation of cycles of selection in Celaya and Morelia during 2011 and in Celaya in 2012. Climatic characterization and agronomic management for both evaluation environments are as follows:

Celaya, Mexico (20º34'N lat 1,760 masl): The climatic conditions for this location are classified as subtropical semiarid, with an annual mean temperature of 18.4 ºC and annual precipitation ranging from 550 to 710 mm.

Morelia, Mexico, (19º42'N lat 1,941 masl): The climatic conditions for this location are classified as subtropical with an annual mean temperature of 17.6ºC and annual mean precipitation of 750 mm. Evaluation plots in both locations and during years were conducted under irrigation, with high input management, with no water restrictions; and using fertilizer, weed and pest control. The applied plant density was 80,000 plants ha^{-1}.

Evaluation trials

Selection cycles 1 to 5 of BWP and BYP, and cycles 1 to 6 of NWP and NYP were evaluated in the experimental trials during 2011. During 2012, cycles 1 to 7 were evaluated of BWP and BYP, and cycles 1 to 8 were evaluated of NWP and NYP. A randomized complete block experimental design with two replications was used in the trials at each location during 2011, and three replications of the trial were conducted in 2012. The combined analysis (two locations in 2011 and one in 2012), was performed only with common genotypes.

Agronomic Traits

For all locations, the grain yield was calculated for each selection cycle for the four populations using the ear and grain weight of each plot, corrected to 14% grain moisture and expressed as ton ha^{-1}. Other agronomic traits that were evaluated include the days at silking and anthesis (recorded when 50% of the plants in a plot were silking and first shedding pollen); furthermore, the plant and ear heights were measured in cm before harvest, from the ground to the flag leaf at the base of the tassel and to the top ear node.

Laboratory Analysis of Oil Content

Samples of seeds representing each cycle, composites of selected families used as the male pollen parent for each selection cycle in the field, were analyzed for oil content at the Center of Biotechnology of Tecnológico de Monterrey.

Selection response in each population was calculated from the first to the improved cycles; in all cases, the selection response was calculated as the difference between the original populations and the selected populations, expressed as a total response and as a percentage per selection cycle, as described below:

Total Response (TR): TR = OC(Cn) - OC(C1)

where: OC(Cn) = Oil content at the improved population; OC(C1) = Oil content at the first cycle the population.

Response expressed as percentage per cycle of selection (R(%) / Cycle):

R(%) / Cycle = [OC(Cn) - OC(C1)] / OC(C1) x 100 / No of Cycles.

A linear regression analysis was also calculated for oil content across cycles, to estimate the incremental rate of each of the four populations, according to the methods described by Gomez and Gomez (1984).

Results

The analysis of variance of grain yield and agronomic traits from the experimental trials conducted during 2011 in Morelia and Celaya, and in Celaya during 2012 along with a combined analysis of both years are presented in Table 1. Only the grain yield and silking date exhibited highly significant values ($P \leq 0.01$) for "Genotype". The anthesis date exhibited a similar response except for Celaya in 2012 and the combined analysis presented highly significant values ($P \leq 0.01$), with the same tendency in Celaya and Morelia during 2011, with significant differences ($P \leq 0.05$). Because the experiments conducted in each environment were composed of genotypes representing different cycles of selection from the four populations, the effects of grain yield were confounded with populations, particularly since in the case of grain yield, the yellow kernel genotypes generally present less grain yield than the white. Additionally the silking and anthesis dates are earlier in the yellow kernel genotypes than genotypes from white populations.

In terms of plant height, significant differences were detected ($P \leq 0.05$) in Morelia in 2011 and Celaya in 2012, and non-significant differentces were determined in the rest of the ANOVAS. This was also true for ear height, where variation was not sufficient to detect significant differences among genotypes in the other environments.

The percent ear husk cover (EC) showed highly significant values ($P \leq 0.01$) in Celaya in 2012 and significant differences ($P \leq 0.05$) in Morelia in 2011. The ear rot percentage presented highly significant values ($P \leq 0.01$) in the combined analysis; and significant differences ($P \leq 0.05$) in both the Morelia and Celaya 2011 environments. Both of these genotype traits responses were highly affected by the interaction with the environment in the evaluation.

In the lower part of Table 1, in the combined ANOVA, the environmental variation indicated that all of the evaluated traits presented highly significant values ($P \leq 0.01$). This can be explained by the different experimental data from each environment because experiments from 2011presented better performance than the 2012 data, whereas the Morelia experiment in 2012 was lost, and the Celaya experiment presented lower performance in all traits.

Table 1 - Mean squares of the analysis of variance of the agronomic traits evaluated at Morelia and Celaya 2011, Celaya during 2012, and the combined analysis across environments. INIFAP Maize Breeding Program.

SV	DF	MF	FF	PH	EH	GY	TSL	EC	ER
					Morelia 2011				
Block	1	0.72	5.12	0.016	0.037	16745841.9	0.56	0.048	046
Genotype	24	6.33*	4.82**	0.021*	0.008NS	8970443**	0.62*	2.38*	1.16*
Error	24	1.3	0.95	0.011	0.007	987677.3	0.23	0.76	0.47
Total	49								
CV (%)		1.44	1.2	4.63	7.54	13.07	39.13	27.23	49.9
					Celaya 2011				
Block	1	0.72	5.78	0.006	0.006	4700791.2	8.35	0.53	0.39
Genotype	24	8.08*	10.90**	0.034NS	0.014NS	1023890.6**	1.75*	0.29NS	2.05*
Error	24	1.80	0.61	0.017	0.022	77813550.8	0.82	0.29	0.64
Total	49								
CV (%)		1.87	1.08	0.017	12.35	8.76	26.07	24.30	30.71
					Celaya 2012				
Block	2	169.36	165.95	6982.17	6730.78	3300656.80		2.53	1.85
Genotype	35	18.77**	18.71**	276.71*	205.68NS	2187311**		0.87**	0.52NS
Error	70	4.31	4.44	208.12	358.88	546811		0.27	0.39
Total	107								
CV (%)		2.74	2.76	5.47	11.95	11.45		17.15	40.24
				Combined Celaya and Morelia, 2011 and Celaya, 2012					
Block	1	37.56	42.96	0.29	0.28	7.91		0.44	0.15
Genotype	22	20.72**	20.71**	0.03NS	0.015NS	7.38**		0.75NS	1.33**
Environment	2	639.18**	887.63**	1.59**	2.26**	350.88**		11.04**	23.03**
Genotype *Env.	44	2.46NS	2.60NS	0.0199NS	0.013NS	2.29*		0.43NS	0.74NS
Error	46	3.84	4.01	0.022	0.028	1.09		0.51	0.50
CV (%)		2.60	2.62	6.21	13.10	11.97		25.94	37.83

SV - source of variation; DF - Degrees of freedom; MF - Male Flowering (days); FF - Female Flowering (days); PH - Plant Height (cm); EH - Ear Height (cm); GY - Grain Yield (Mg ha^{-1}); TSL - Total Stalk Lodging (%); EC - Ear Coverage (%); ER - Ear Rot (%). * - significant at $P \leq 0.05$; ** - significant at $P \leq 0.01$; NS - Not significant.

To illustrate the response through the selection cycles of each of the four populations, Tables 2 to 5 summarize the performance of grain yield and agronomic characteristics over environment. The response of the HOC recurrent selection cycles for BYP is presented in Table 2, indicating grain yield and other agronomical traits from different evaluation environments. According to the mean comparison values (LSD $P \leq 0.05$), the combined analysis of each trait exhibits no statistical changes across the selection cycles. Nevertheless, it is important to highlight the tendencies of the grain yield and the agronomic variables in this population. With respect to grain yield, the values over selection cycles in each environment, indicate higher grain yields at Celaya in 2011 and lower performance in Morelia in 2011 and Celaya in 2012. In the combined analysis across locations the grain yield exhibits a very small positive genetic gain (ΔG) and the LSD value exhibits bigger gains than the differences over selection cycles, which indicates that the grain yield was not affected from oil content increases. With respect to anthesis and silking dates, and plant and ear height, according to the LSD values these traits did not exhibit significant differences in the selection process in this population. Furthermore, ΔG for these traits presented very small negative values which indicates that over the selection process this population remained at the same maturity and plant height. The combined analysis of all traits indicated that the only source of variation that presented highly significant values was the environment, which can be explained by looking at the variation response of the traits observed between each individual environment. The gain in recurrent selection for oil content in BYP

Table 2 - Response of grain yield and agronomic traits in different environments, over the cycles of recurrent selection, toward increasing the oil content in the Bajio Yellow Population (BYP).

	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celay 2012	Comb	
Cycles																					
	Grain Yield (Mg ha^{-1})				Anthesis (days)				Silking (days)				Plant Height (cm)				Ear Height (cm)				Oil Content (%)
C1	5.34	9.98	6.33	7.22	77	69	73	73	79	69	74	74	217	218	257	230	109	115	170	131	5.30 ± 0.12
C2	5.66	11.78	5.20	7.55	77	71	72	73	79	70	73	74	220	240	258	239	115	128	168	137	5.80 ± 0.10
C3	6.05	10.82	5.06	7.31	78	70	71	73	79	71	72	74	212	208	252	223	106	110	142	119	6.10 ± 0.56
C4	5.67	10.78	5.76	7.40	78	69	72	73	80	70	73	75	216	228	2650	236	115	118	160	131	6.60 ± 0.12
C5	6.65	9.58	6.12	7.45	77	69	72	72	79	69	73	74	222	220	253	231	110	128	140	126	7.30 ± 0.06
C6			5.40				72	-	-	-	72		-	-	255	-	-	-	148	-	7.50 ± 0.09
C7			6.26				73	-	-	-	74		-	-	265	-	-	-	160	-	7.50 ± 0.07
ΔG				0.03				-0.12				-0.06				-0.03				-1.71	
LSD (0.05)				1.39				2.79				2.70				20				17	
Genotype				77107.10^{NS}				0.77^{NS}				0.32^{NS}				0.02^{NS}				0.03^{NS}	
Environment				76028746.6^{**}				160.07^{**}				222.17^{**}				0.39^{**}				0.57^{**}	
G*E				1399395.10^{NS}				1.16^{NS}				1.38^{NS}				0.01^{NS}				0.0^{NS}	

*- significant at $P \leq 0.05$; ** - significant at $P \leq 0.01$; NS - Not significant. C1, C2, C3….Cn - recurrent selection cycles of to increase oil content.

Table 3 - Response of grain yield and agronomic traits in different environments, during recurrent selection cycles, toward increasing the oil content in the Northwest Yellow Population (NYP).

Cycles	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celay 2012	Comb	
	Grain Yield (Mg ha^{-1})				Anthesis (days)				Silking (days)				Plant Height (cm)				Ear Height (cm)				Oil Content (%)
C1	6.39	11.53	5.94	7.95	81	72	76	76	82	73	77	77	217	225	277	239	107	125	170	134	4.90 ± 0.10
C2	5.96	11.71	6.89	8.19	80	72	76	76	82	74	77	77	215	245	262	240	111	135	162	136	5.80 ± 0.17
C3	6.61	11.27	6.46	8.12	81	71	75	76	83	71	76	76	217	235	263	238	106	118	158	127	5.90 ± 0.27
C4	7.36	13.03	6.57	8.99	80	74	75	76	83	75	76	78	217	250	282	249	102	130	160	131	6.10 ± 0.38
C6	6.78	12.00	6.88	8.56	79	71	76	75	80	71	77	76	228	238	255	240	114	123	152	129	7.50 ± 0.11
C7	-	-	6.03	-	-	-	74	-	-	-	73	-	-	-	258	-	-	-	155	-	7.60 ± 0.07
C8	-	-	6.40	-	-	-	74	-	-	-	74	-	-	-	255	-	-	-	158	-	8.10 ± 0.15
ΔG				0.20				-0.25				-0.29				1.05				-1.47	
LSD (0.05)				0.90				2.29				2.14				14				19	
Genotype				1419354.30^{NS}				1.75^{NS}				4.47^{NS}				0.02^{NS}				0.01^{NS}	
Environment				94228874.1**				164.03**				216.40**				0.49**				0.54**	
G*E				683440.70^{NS}				1.67^{NS}				3.13^{NS}				0.02^{NS}				0.01^{NS}	

*- significant at P ≤ 0.05; ** - significant at P ≤ 0.01; NS - Not significant. C1, C2, C3….Cn - recurrent selection cycles of to increase oil content.

can be observed in the last column of Table 2, which after seven cycles of selection shows a total kernel oil content of this population reached 7.5%.

Table 3 shows the response of the process of recurrent selection for HOC in NYP; In this yellow kernel population the selection cycles also exhibited no significant difference in grain yield, maturity or plant height based on the LSD values. The ΔG of these variables was also very small, with positive values for grain yield and plant height and negative for the other traits. The environmental source of variation of the combined analysis presented statistically values which were explained by the contrasting evaluation environments. In the last column of Table 3, this population can be represent the highest value of oil content of the four studied populations.

The Recurrent selection response in BWP is presented in Table 4, where grain yield silking and anthesis dates, and plant and ear height, can be seen to have a non-significant response across the cycles for all traits was according to the LSD (P ≤ 0.05) values. For all traits, ΔG presented very small positive values, which can be interpreted as this population not presenting significant changes, whereas the kernel oil content increased through selection cycles. In this table, it is also possible to observe that the variation response of the cycles across locations is responsible for the highly significant values resulting from environmental variations.

The response of the recurrent selection cycles for HOC in NWP at each location and across locations is presented in Table 5. In this white kernel population a higher grain yield potential compared with the other three populations, was observed; this was specifically the case at Celaya in 2011, where the sixth of selection cycle yielded 13.21 ton ha^{-1}. With respect to all of the evaluated traits, NWP maintained similar tendencies as the other populations, and similar statistical values across cycles of selection can be observed according to the LSD (P ≤ 0.05) values. With respect to the ΔG, it was also negligible in this population, which might be due to non-significant changes that occurred while the kernel oil content increased. In the combined analysis for environmental variations, highly significant differences were present for all traits, and, in the case of the silking date, the genotype and the interaction genotype x environment also presented highly significantly different values.

A comparison of the four populations indicates that the locations with the highest and lowest grain yields across the cycles among the four populations were Celaya 2011 and Celaya 2012 respectively. The low performance during 2012 is attributed to climate conditions and the planting date. In comparing the combined analysis of grain yield among the selection cycles among the four populations, the white kernel populations (Tables 4 and 5) presented higher grain yields (approximately 9 ton ha^{-1}) compared to their yellow counterparts (Tables 2 and 3).

The last columns of Tables 2 to 5 depicts the kernel oil content gain across recurrent selection cycles for the BYP, NYP, BWP, and NWP subtropical populations. A similar tendency occurred with increasing oil contents across recurrent selection cycles among the four studied HOC populations. However, the selection response in each population was somehow different mainly due to their differing genetic backgrounds.

According to the mean comparison information, the LSD values and tendencies in each environment related to the days to anthesis and silking, which is depicted in Tables 2 to 5, did not exhibit significant differences across cycles. This means that the proposed selection process for HOC did not modify the earliness in any of the four populations.

Comparing the environments values, the plant height over the selection cycles in the four populations exhibited higher plants in Celaya 2012. An opposite response was observed in Morelia where the plants were shorter almost in all cycles.

The oil content responses throughout the recurrent selection cycles for the BYP, NYP, BWP, and NWP populations are summarized in Table 6. The proposed selection program throughout the study years increased significantly the average kernel oil content among the four populations. Because the

Table 4 - Response of grain yield and agronomic traits in different environments, during recurrent selection cycles of, toward increasing the oil content in the Bajio White Population (BWP).

Cycles	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celay 2012	Comb	
	Grain Yield (Mg ha^{-1})				Anthesis (days)				Silking (days)				Plant Height (cm)				Ear Height (cm)				Oil Content (%)
C1	6.38	11.63	7.30	8.44	78	70	77	75	81	71	78	77	216	225	275	239	112	113	165	130	5.70 ± 0.08
C2	7.13	11.92	7.05	8.70	78	71	77	75	82	71	78	77	230	233	278	247	114	115	168	132	6.00 ± 0.05
C3	7.95	11.65	7.49	9.03	78	72	74	74	80	72	75	75	233	235	265	244	116	135	150	134	6.10 ± 0.20
C4	7.68	11.27	7.02	8.65	78	72	77	76	80	73	78	77	252	210	277	246	127	118	170	138	6.10 ± 0.31
C5	8.03	10.82	6.90	8.58	78	73	75	75	80	73	77	77	230	235	263	243	115	118	158	130	7.10 ± 0.35
C6	-	-	6.54	-	-	-	76	-	-	-	78	-	-	-	268	-	-	-	165	-	7.50 ± 0.07
C7	-	-	6.65	-	-	-	77	-	-	-	79	-	-	-	262	-	-	-	145	-	7.60 ± 0.05
ΔG				0.02				0.12				0.02				0.78				0.71	
LSD (0.05)				1.18				2.11				2.41				14.52				22.09	
Genotype				298863.30^{NS}				2.38^{NS}				3.53^{NS}				0.01^{NS}				0.01^{NS}	
Environment				54988689**				108.00**				187.15**				0.59**				0.67**	
G*E				585916.50^{NS}				3.27^{NS}				3.69^{NS}				0.03^{NS}				0.01^{NS}	

*- significant at $P \leq 0.05$; ** - significant at $P \leq 0.01$; NS - Not significant. C1, C2, C3….Cn - recurrent selection cycles of to increase oil content.

seed of the original cycle (C0) from the four populations was not available for this study, the oil content of kernels from the first cycle (C1) was used as the initial oil content. Three of the four populations belonging to the first cycle appeared to be higher in oil compared to regular commercial counterparts. However, it was observed that the four maize populations exhibited an important selection advance for oil content because kernels belonging to the most advanced cycles contained from 1.9% to 3.2% more oil compared to kernels assayed during the first cycle.

Even though the Northwest populations have an additional breeding selection cycle, the kernels harvested during the last cycle of NWP comparatively contained the lowest oil content (6.7%). On the other hand, the NYP kernels contained the highest (8.1%) oil amount. This specific population increased its oil content by 0.4% for each selection cycle with a total increment of 3.2%. Likewise, the increment of oil for kernels belonging to the BYP, BWP, and NWP populations by cycle were 0.31%, 0.27%, and 0.30%, respectively. The average HO selection process response among the four populations presented at the bottom of Table 6, with a 2.43% total increment and an average of 0.32% incremental increase by cycle. The NYP population presented the highest slope (b) = 0.4393x for the selection response. The other yellow kernel population, BYP presented a slightly lower slope value of 0.4000 in the selection response by cycle compared with the two white kernel populations with slopes of 0.3464 for BWP and 0.2988 for NWP. In general according to the information presented herein, the white kernel populations had a lower increment of oil content compared to the yellow kernel populations. The estimated correlation coefficients (R^2) values for BYP, NYP, and BWP were 0.9555, 0.9685, and 0.9012 respectively, which was highly significant ($P \leq 0.1\%$); for NWP the (R^2) value was 0.8032 with a significance of $P \leq 0.5\%$. According to Gomez and Gomez (1984), the observed R^2 values can be interpreted as having a linear response to selection for oil content in among the four populations.

Discussion

Because the oil content in maize kernels has a high heritability (Hallauer and Miranda, 1981), and because oil in maize responds to additive genetic control (Silvela et al, 1989), a recurrent selection scheme was implemented with the aim of increasing the oil content in four subtropical maize populations. A reduction in the grain yield, and changes in other agronomic traits were avoided. The results presented herein clearly indicate that the proposed response of recurrent selection among the four populations across environments did not affect the grain yield, earliness and other related agronomic traits but clearly increased the kernel oil content. The four populations matured later in Morelia in 2011 due to the higher altitude and average temperature at the location. Furthermore, differences were manifested due to genetic background of each population, as yellow kernel populations matured earlier and had lower grain yield potential compared to the white populations. Additionally, populations from Bajio matured earlier (Tables 2 and 4) than populations from the Northwest (Tables 3 and 5). The NWP matured latest, probably because the Northwest White Population contained more tropical germplasm, which in subtropical environments tended to mature later.

In Celaya in 2012 higher plants were consistently observed likely due to a later planting date (June 29th) which also affected the grain yield. According to Cirilo and Andrade (1996), plants tend to be taller and grain yields lower with later planting dates due to environmental conditions, the temperature in particular. An opposite response was observed in Morelia, where plants in almost all cycles were shorter.

For all of the variables in each environment, no significant differences among cycles was observed, which means that populations maintained their agronomic characteristics including grain yield, through the process of selection aimed to increase oil content. Although the four populations had different genetic backgrounds, they showed a similar selection response for all of the studied traits while the selec-

Table 5 - Response of grain yield and agronomic traits in different environments, over the cycles of recurrent selection, toward increasing the oil content in the Northwest White Population (NWP).

Cycles	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celaya 2012	Comb	Morelia 2011	Celaya 2011	Celay 2012	Comb	
	Grain Yield (Mg ha^{-1})				Anthesis (days)				Silking (days)				Plant Height (cm)				Ear Height (cm)				Oil Content (%)
C1	9.37	12.31	6.26	9.31	81	74	78	78	82	76	78	78	231	215	262	236	114	105	162	127	4.30 ± 0.20
C2	8.59	13.46	5.46	9.17	82	75	79	79	83	76	78	79	232	258	252	247	114	133	153	133	5.40 ± 0.03
C3	8.70	12.86	5.53	9.03	80	75	80	78	83	76	81	80	232	253	258	247	116	128	153	132	5.70 ± 0.16
C4	8.46	13.09	5.83	9.13	82	74	80	78	84	75	81	80	239	225	265	243	113	115	163	130	5.80 ± 0.10
C5	9.91	12.93	6.22	9.68	81	74	78	78	83	75	78	79	247	245	273	255	122	120	162	134	6.00 ± 0.45
C6	9.46	13.21	6.46	9.71	81	75	78	78	82	75	78	78	232	235	267	244	122	125	160	136	6.90 ± 0.20
C7	-	-	6.86	-	-	-	78	-	-	-	78	-	-	-	263	-	-	-	167	-	6.30 ± 0.03
C8	-	-	7.11	-	-	-	79	-	-	-	80	-	-	-	263	-	-	-	158	-	6.70 ± 0.11
ΔG				0.10				-0.05				-0.02				1.79				1.31	
LSD (0.05)				0.56				0.97				1.00				14.90				14.09	
Genotype				644838.70 NS				1.39 NS				3.25**				0.02 NS				0.00 NS	
Environment				146811053.6**				121.02**				158.52**				0.28**				0.50**	
G*E				428756.6 NS				1.06 NS				1.97**				0.03 NS				0.01 NS	

*- significant at P ≤ 0.05; ** - significant at P ≤ 0.01; NS - Not significant. C1, C2, C3….Cn - recurrent selection cycles of to increase oil content.

tion process for HOC occurred.

Grain yield tendencies across the selection cycles among the four populations were opposite the responses previously documented by Alexander and Seif (1963), Misevic and Alexander (1989), Dudley et al (1974; 1977), and Rosulj et al (2002), who reported a negative correlation between grain yield and kernel oil content by selection cycle.

We attribute the observed non-significant statistical response to the special care in selection from the field where healthy plants with no-lodging, intermediate height and larger ears were carefully selected.

Among the four populations studied herein the average kernel oil content response by cycle was 0.32%. This value is lower than the average of 0.77% from five populations reported by Song and Chen (2004). These authors bred other populations and their estimated values came from selection differentials, not from the performed selection response. Furthermore, they used smaller population sizes, which may be a cause of the reported significant reduction in kernel starch.

In the overall selection response across cycles in NWP (Table 5), no significant differences were detected for grain yield, even though a slight tendency to increase grain yield through progressive cycles was observed; earliness and plant and ear heights were maintained across the cycles. In relation to the other agronomic variables (data not shown) studied, the percent lodging presented a small tendency toward reduction, whereas rot ears, husk coverage and infestation with fusarium did not present important significant differences across the cycles. Although the NWP oil content selection response presented a positive gain, a tendency toward lower values was observed across cycles, while the grain yield presented higher values in different environments, compared with other populations.

Similar selection response tendencies were presented for the other three populations (BWP, NYP, and BYP) in almost all of the studied variables which did not show statistically significant changes.

In conclusion, an effective selection response for HOC was obtained in the four populations, with a gradual gain of oil by cycle of 0.31%, 0.40%, 0.27%, and 0.30% for BYP, NYP, BWP, and NWP, respectively. These maize populations contained final oil content of 7.5%, 8.1%, 7.6%, and 6.7%, for BYP, NYP, BWP, and NWP, respectively. Moreover, the results at each location and across locations indicate that among the four populations grain yield was not affected across selection cycles as kernel oil content increased. The application of selection criteria which emphasized top yielding and agronomicalyl superior individuals from each population was highly efficient. This strategy avoided yield reduction over cycles of selection for HOC. Importantly, other traits such as earliness, plant and ear height, and other agronomic characteristics showed no-significant changes.

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Table 6 - The oil content recurrent selection response in BYP, NYP, BWP and NWP subtropical populations; the total and cycle oil increment percentages, and estimated regression values.

Population	Number of Cycles	First Cycle Oil content (%)	Last Cycle Oil content (%)	Total Response (%)	Oil increment by Cycle (%)	R (%) / Cycle	Estimated linear regression equation[§]	R^2#
BYP	7	5.3	7.5	2.2	0.31	4.19	Y= 4.9858 + 0.4000 x **	0.9555**
NYP	8	4.9	8.1	3.2	0.40	4.93	Y= 4.6107 + 0.4393 x **	0.9685**
BWP	7	5.7	7.6	1.9	0.27	3.57	Y= 5.0200 + 0.3464 x **	0.9012**
NWP	8	4.3	6.7	2.4	0.30	4.48	Y= 4.5429 + 0.2988 x **	0.8032*
Average		5.05	7.47	2.43	0.32	4.29		

[§] t distribution of probability,** (P ≤ 0.001). [#] R^2 (Correlation coefficient) - ** (P ≤ 0.01) and * (P ≤ 0.05).

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