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Fatty acid composition of high oleic sunflower hybrids in a changing environment

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ABSTRACT

High oleic hybrids of sunflower are widely cultivated around the world. The effect of temperature on oleic acid percentage of these hybrids is a concern, since oils with oleic acid percentage above a threshold receive a prime over the regular price. The objective of this work was to identify the main avenues for the genetic improvement of oleic acid percentage of high oleic hybrids of sunflower, both in current and future global warming scenarios. A data set obtained in a trial network allowed to explore the oleic acid percentage response to temperature of high oleic hybrids in the argentine sunflower growing region (between 29 and 38° LS, 46 trials in 15 locations during the period 2005/06–2012/2013). A similar data set was used to evaluate the variability in phenology. Mean values and stability across environments of oleic acid percentage differed among the studied high oleic hybrids. Differences in the parameter values of a sigmoid equation evidenced the variability in the response of oleic acid to temperature. Oleic acid percentage was simulated with a model that included this equation coupled to a phenology module, for different sowing dates and locations with contrasting temperature, under current conditions and a global warming scenario. It was possible to identify a low number of temperatures and field environments useful to reproduce the rankings of hybrids obtained with a wide range of temperatures. This information could be used to phenotype for high oleic percentage with a low number of experiments and reduce the efforts to identify better high oleic genotypes. Simulations show that the maximum oleic acid percentage is currently not attained in 50% of the studied hybrids in some sowing dates, even at the warmest locations, while in a future global warming scenario it would not be attained in 30% of the studied hybrids in the colder locations. Sensitivity analysis was performed for parameters of the sigmoid equation and the phenology module determining when the critical period for fatty acid composition occurs. In both in current and future scenarios, phenology parameters showed a null or low effect on oleic acid percentage. Two parameters of the sigmoid equation showed a significant impact, which differed between current and future scenarios. Simulations suggest that the stability of oleic acid percentage could still be a concern in the future. However, selecting for key parameter values for a given scenario could help to obtain better high oleic hybrids of sunflower.

1. Introduction

The gene pool of cultivated sunflower (*Helianthus annuus* L.) has been subjected to intense selection for a specific oil composition (Putt, 1997; Burke et al., 2005). For oil quality purposes, oleic and linoleic are the most important fatty acids because they constitute almost 90% of the total fatty acids in sunflower oil. Sunflower fatty acid composition has been modified by breeding and mutagenesis (Fernández-Martínez et al., 1989; Lagravère et al., 1998; Lacombe

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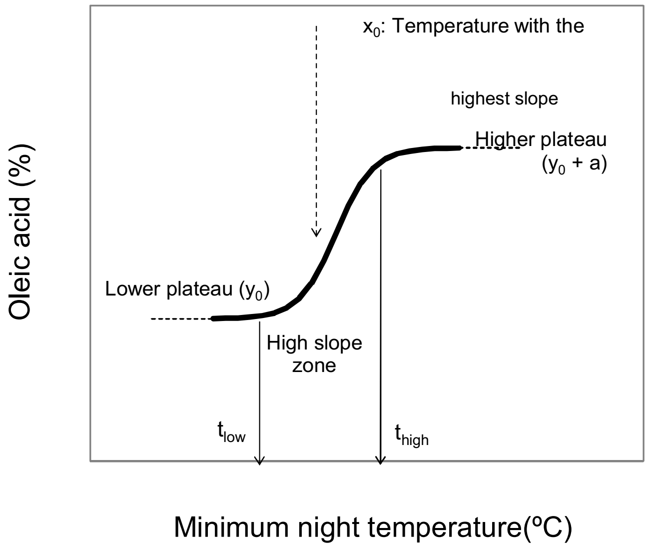

Fig. 1. Schematic representation of the response of oleic acid percentage to minimum night temperature during the 100–300 °C day after flowering period and some parameters useful to compare the response of different hybrids (from Izquierdo and Aguirrezábal, 2008).

and Bervillé, 2000; Haddadi et al., 2013), and high oleic cultivars with oleic acid (OA) percentage above 80% have been obtained. Currently, the area sown with high oleic hybrids has increased to almost 2 million hectares, representing about 11% of the total sunflower area around the world (Labalette et al., 2012).

Stability of fatty acid composition across environments is generally higher for high oleic hybrids than traditional ones (Izquierdo et al., 2002). However, high oleic hybrids showed differences in their response to the environment and their maximum oleic acid percentage attainable (Triboï-Blondel et al., 2000; Luquez et al., 2002; Roche et al., 2006). Although the effect of the environment on fatty acid composition in these genotypes is smaller than in traditional ones, it can still be a concern, especially with strict oil market standards, since oils with oleic acid percentage above a threshold receive a prime over the regular price.

Models have long been used to describe, analyze and predict the response of plant traits to the environment (Jones, 2014). They can range from detailed mechanistic descriptions to simple response curves to environmental variables, which represent “meta-mechanisms” at the plant or crop level (Tardieu, 2003). If models are robust enough, one set of parameters represents one genotype (Hammer et al., 2006), and thus they can be used to analyze complex traits with significant genotype by environment interaction or pleiotropic effects. Given the same functional expression characterizing the response of several hybrids, the analysis of the variability of model parameters provides important information about the nature of the observed genotype by environment interactions and provides new traits (parameters) that are independent of the environment.

Oleic acid percentage in sunflower oil is closely related to minimum night temperature during a short period during grain filling (between 100 and 300 °C days after flowering; MNT; base temperature 6 °C). The response of oleic acid percentage to minimum night temperature (MNT) follows a sigmoid function (Izquierdo and Aguirrezábal, 2008, Fig. 1), and is subjected to genetic variability among traditional hybrids as evidenced by differences in the parameters of this function (minimum and maximum attainable oleic acid percentage, maximum slope and range of temperatures in which oleic acid percentage changes with temperature). The only high oleic hybrid tested so far showed lower sensitivity to temperature as evidenced by smaller difference between the parameters for minimum and maximum oleic acid percentage (Izquierdo and Aguirrezábal, 2008). Up to date, whether this model is also useful for analyzing the variability among genotypes with modified fatty acid composition is unknown.

As previously described, oleic acid percentage in traditional hybrids of sunflower showed a continuous, nonlinear response to temperature during a specific period late in the crop growth cycle. For a given sowing date, the rate of crop development determines the moment of the year in which this process occurs. Since temperature also affects the rate of crop development in a nonlinear fashion (Parent and Tardieu, 2012), it becomes difficult to predict the outcome of an increase in temperature on oil quality. Many works evidence the effect of climate variability and global warming on plant development and their interactions with different plant processes, both by empirical measurements and simulations (Chmielewski and Rötzer, 2001; Sadras and Monzon, 2006; Pereyra-Irujo and Aguirrezabal, 2007). Moreover, crop development and oil fatty acid composition are related to different temperature variables (daily mean or minimum night temperature, respectively), which are expected to be differently affected by global warming (Rusticucci and Barrucand, 2004).

Identifying which parameter of the sigmoid function relating oleic acid percentage to temperature could have the highest impact on oil composition when modified, could be valuable information for the improvement of sunflower oil quality (Aguirrezábal et al., 2014). Moreover, simple models that simulate the whole crop cycle (e.g. Pereyra-Irujo and Aguirrezábal, 2007) could be useful for analyzing complex processes, such as the interaction of different temperature variables (i.e. minimum, mean, and maximum) on the determination of crop development and fatty acid composition. Also, phenotyping has become a bottleneck for further genetic improvement, especially of complex traits, because it can be often technically difficult, expensive, or time consuming (Hall and Richards, 2013). The use of such models could be helpful to identify key temperatures and environments for phenotyping oleic acid percentage of high oleic hybrids of sunflower. The objective of this work was to identify the main avenues for the genetic improvement of oleic acid percentage of high oleic hybrids of sunflower, both in current and future global warming scenarios.

2. Materials and methods

2.1. Experiments

A first data set, originated from the Argentine National Trial Network of Commercial Sunflower Hybrids (INTA), allowed exploring the response of oleic acid (OA) percentage to temperature in high oleic hybrids grown throughout the Argentine sunflower growing region (between 29 and 38° S; Table 1), with minimum night temperature (MNT) values ranging from 12.9 to 21.2 °C. The data set included 46 trials in 15 locations during the period 2005/2006–2012/2013 (Table 1).

Hybrids were laid out in randomized complete-block or alpha-lattice designs, with three replicates. Seventeen commercial hybrids were selected and considered for analysis (Table 1). A plot size of three or four rows 5.5 m long and inter-row spacing of 0.50 or 0.70 m was used. The plots were over-planted and later thinned to 45,600–55,000 plants ha^{-1}. Mostly no-tillage sowing was used in the trials. Weeds, insects and pests were controlled chemically or mechanically. All trials were conducted under rainfed conditions and nutrient deficiencies were overcome through fertilization. Sowing dates were as close as possible to the optimum recommended for each location. Time to anthesis was defined as the moment when 50% of the plot plant population reached full anthesis (R-5.5, Schneiter and Miller, 1981).

Table 1
Locations and hybrids evaluated in the National Trial Network of Commercial Sunflower Hybrids (INTA).

Location—Province	Latitude	Experimental Crop Season	Selected hybrids
Trials used to evaluate oleic acid variability			
Anguil, La Pampa	36° 32′	2008/09	ACA862HO[1], Aromo105[2], Aromo11[2], BS90INTA[3], BS92INTA[3], SRM822[4], SRM840[4]
Balcarce, Buenos Aires	37° 52′	2005/06, 2006/07, 2007/08, 2008/09, 2009/10, 2010/11, 2011/12, 2012/13	ACA862HO, ACA866[1], Aromo105, Aromo 11, Atomic[5], BS92INTA, DK3945OP[6], NTO1.0[7], NTO4,0[7], Olisun[8], Olisun2[8], SerranoAO[9], Sierra[10], SPS3200AO[5],SRM822, SRM840
Bulnes, Córdoba	33° 31′	2012/13	Serrano,
Chacra Barrow, Buenos Aires	38° 19′	2005/06, 2006/07, 2007/08, 2008/09, 2009/10, 2010/11, 2011/12, 2012/13	AC886, Aromo 105, Aromo11, DK3945OP, NTO1.0, NTO4.0, Serrano, Sierra, SPS3200AO, SRM822, SRM840
Chacra Bellocq, Buenos Aires	35° 22′	2006/07, 2008/09	ACA862HO, ACA866, Aromo11, Atomic, DK3945OP, Olisun, Olisun2, Sierra
Huinca Renancó, Córdoba	34° 50′	2011/12, 2012/13	BS90INTA, BS92INTA, DK3945OP, Serrano
Manfredi, Córdoba	31° 50′	2005/06, 2006/07, 2007/08, 2008/09, 2009/10, 2010/11, 2011/12, 2012/13	ACA862HO, ACA866, Aromo 105, Aromo 11, Atomic, BS90INTA, BS92INTA, DK3945OP, NTO4.0, Olisun, Olisun2, Serrano, Sierra, SPS3200AO, SRM840,
Mercedes; Corrientes	29° 11′	2008/09	BS92INTA, DK3945OP
Miramar, Buenos Aires	38° 15′	2012/13	ACA866, Aromo 105, DK3945OP, NTO1.0, NTO4.0
Paraná, Entre Ríos	31° 44′	2006/07, 2007/08,	ACA862HO, Atomic, Olisun, Olisun2, Sierra, SPS3200AO, SRM822, SRM840
Pergamino, Buenos Aires	33° 54′	2008/09, 2012/13	Aromo 105, Aromo11, BS90INTA, DK3945OP, NTO4.0, Olisun2
Reconquista, Santa Fe	29° 09′	2006/07, 2007/08, 2008/09, 2009/10, 2010/11, 2011/12, 2012/13	ACA866, Aromo11, Atomic, BS90INTA, BS92INTA, DK3945OP, NTO4.0, SerranoAO, Sierra, SPS3200AO, SRM840
San Miguel del Monte, Buenos Aires	35° 25′	2010/11	NTO1.0, NTO4.0
Tandil, Buenos Aires	37° 19′	2012/13	ACA866, Aromo 105, NTO1.0
Vicuña Mackena, Córdoba	33° 55′	2011/12	BS90INTA, BS92INTA, DK3945OP
Trials used to evaluate phenology variability			
Anguil, La Pampa	36° 32′	2008/09, 2010/11, 2011/12, 2013/14	ACA862, AROMO11, DK3845, NTO4.0, OLISUN2, SRM822, SRM840
Ascasubi, Buenos Aires	37° 51′	2006/07, 2007/08, 2008/09, 2009/10, 2010/11, 2011/12	ACA862, AROMO11, DK3845, NTO1.0, NTO4.0, OLISUN, OLISUN2, SERRANO, SIERRA, SPS3200, SRM822, SRM840
Balcarce, Buenos Aires	38° 23′	2006/07, 2007/08, 2008/09, 2009/10, 2010/11, 2011/12	ACA862, AROMO11, DK3845, NTO1.0, NTO4.0, OLISUN, OLISUN2, SIERRA, SPS3200, SRM822, SRM840
Barrow, Buenos Aires	38° 23′	2006/07, 2008/09, 2009/10, 2010/11, 2011/12, 2012/13	ACA862, AROMO11, DK3845, NTO4.0, OLISUN, OLISUN2, SIERRA, SPS3200, SRM822, SRM840
Chacra Bellocq, Buenos Aires	31° 50′	2006/07, 2007/08, 2008/09, 2009/10, 2012/13	ACA862, ACA866, DK3845, NTO4.0, OLISUN, OLISUN2, SERRANO, SIERRA, SPS3200, SRM822, SRM840
Bordenave, Buenos Aires	31° 44′	2006/07, 2007/08	DK3845, OLISUN, OLISUN2, SIERRA, SPS3200, SRM840
Ceres, Santa Fe	33° 53′	2008/09, 2010/11, 2011/12, 2012/13	ACA862, AROMO11, DK3845, NTO4.0, OLISUN2
Cnel Suarez, Buenos Aires	26° 00′	2006/07, 2007/08	DK3845
La Tigra, Chaco	29° 09′	2006/07, 2007/08, 2008/09, 2009/10, 2011/12, 2012/13	ACA862, ACA866, AROMO11, DK3845, NTO4.0, SERRANO, SIERRA, SPS3200, SRM822, SRM840
Manfredi, Córdoba	37° 20′	2010/11	AROMO11, DK3845

Seed companies: [1]Asociación de Cooperativas Argentinas ACA S.A., Pergamino, Buenos Aires, Argentina; [2]Nidera S.A., Junín, Buenos Aires, Argentina; [3]Biosol Semillas, Balcarce, Argentina; [4]Sursem. S.A:, Pergamino, Buenos Aires, Argentina; [5]SPS Argentina S.A., Buenos Aires, Argentina. [6]Monsanto Argentina S.A.I.C., Mar del Plata, Buenos Aires, Argentina; [7]Dow Agrosciences Argentina S.A., Colón, Buenos Aires, Argentina; [8]Advanta S.A.I.C., Junín, Buenos Aires, Argentina; [9]Produsem S.A., Pergamino, Buenos Aires, Argentina; [10]Seed 2000 Argentina S.R.L., Venado Tuerto, Santa Fe, Argentina.

Before all florets from the capitulum outer ring showed their stamens, three to five representative plants per plot were marked for sampling and their capitulum was covered with a pollination bag (Delnet, Rosario, Argentina) to avoid cross-pollination between different hybrids.

A second data set, also provided by the National Trial Network of Commercial Sunflower Hybrids (INTA), was used to evaluate the variability in phenology among 13 high oleic hybrids, spanning a range of latitudes similar to that of the first data set (Table 1). Management was similar to that of the experiments in the first data set.

2.2. Sample processing and chemical analysis

Covered capitula from the first set of experiments were sampled and oven-dried with circulating air at 60 °C. Grains between rings 4 and 19 of the capitulum were manually separated in order to determine fatty acid composition of grains set at a similar date and, therefore, exposed to similar environmental conditions (Izquierdo et al., 2002). Only non-empty grains (kernel occupying at least 20% of total space in the grain) were used. Oil extraction and methylation were performed following the technique proposed by Sukhija and Palmquist (1988). Fatty acid composition was determined by gas chromatography (GLC, Varian 3400). The concentration of each fatty acid was expressed as percentage of the total fatty acids identified in the oil.

2.3. Oleic acid percentage data analysis

Relationships between OA percentage and MNT were analyzed according to a previously published sigmoid relationship (Izquierdo and Aguirrezábal, 2008). Mathematical equation of such function is

$$\%\mathrm{AO} = y_0 + \frac{\alpha}{\left(1 + \mathrm{Exp}^{\left(\frac{-(x-x_0)}{b}\right)}\right)} \tag{1}$$

where y_0 (%) is the lowest OA percentage, a is the difference between the minimum and the maximum OA percentage, x (°C) is the MNT during the period 100–300 °C day after flowering, x_o (°C) is the temperature at which the slope is highest, and b is the parameter defining the degree of curvature of the function (Fig. 1).

The genetic variability of the response of OA percentage to temperature among the genotypes of the first data set was evaluated by analyzing y_0, and the derived parameters y_{max} (the highest OA percentage, calculated as $y_{max} = y_0 + a$), and b_{max} (the highest slope, calculated as $b_{max} = (a \times b^{-1})/4$).

In order to obtain estimates of the variability of each parameter that could allow us to compare the values of the parameters among hybrids a "bootstrap" analysis was conducted as described by Izquierdo et al. (2006). For each hybrid, data were resampled 100 times and Eq. (1) was fitted to each resampled data set, thus obtaining 100 values for each parameter from the original data set. All the fittings were performed with Microsoft Excel and the Sigmaplot 8.0 software.

Theoretical rankings were generated by calculating OA percentage every 0.5 °C within a range of temperature (from 14.0 to 20.5 °C), spanning 95% of the temperatures observed in experimental data. Hybrids were ranked according to: (i) mean OA percentage values (ii) OA percentage at each individual temperature (iii) mean OA percentage at two temperatures and (iv) mean OA percentage at three temperatures. Correlation analyses were performed in order to compare the different rankings obtained.

2.4. Phenology data analysis

In order to consider the possible effects of phenology on oil quality in different genotypes, a model was constructed by combining an oil quality module (based on Eq. (1)) with a phenology module that allows estimating flowering time (and therefore the 100–300 °C day after flowering period) from temperature and photoperiod at sowing. The rate of development was assumed to follow a Arrhenius-type function with temperature, according to the model of Parent and Tardieu (2012). Daily minimum and maximum temperatures were converted to hourly temperatures according to the Parton and Logan (1981) model, and hourly developmental rates were integrated to obtain a "days at 20 °C" equivalent value for each day. The number of days (at 20 °C) to flowering was related to photoperiod following a sigmoid function, as in Pereyra-Irujo et al. (2009). Model parameters were fitted to the second data set, which included 13 of the genotypes from the first data set. Parameters describing the inflection point and curvature of the sigmoid function were fitted for a pool of all genotypes, while the maximum and minimum days to flowering (i.e., at short and long photoperiods) were fitted for each genotype. In three of these genotypes (NTO 1.0, Olisun and Olisun 2) there were no data available for photoperiods shorter than 12 h; in those cases, the effect of photoperiod (in days at 20 °C) was assumed to be equal to that of the average of all genotypes.

2.5. Simulations

Using this combined model, the flowering date, the date of the 100–300 °C day after flowering period, and the OA percentages of 13 genotypes (those for which parameters for both oil quality and phenology were fitted) under different conditions were simulated. Three locations (Sáenz Peña, Paraná, and Balcarce), representing different zones of the sunflower growing region of Argentina, were considered (Hall et al., 2013), as shown in Fig. 2. Three sowing dates were used for each location, which represent early, intermediate, and late sowings for each region (Sáenz Peña: Jul 15, Aug 18, Sept 30; Paraná: Sept 1, Oct 10, Nov 20; Balcarce: Sept 20, Oct 10, Nov 11: Aguirrezábal et al., 2001). The model was run with average daily weather data for the 1980–1999 period, and with regional climatic projections for the 2080–2099 period according to emission scenario A1B (Christensen et al., 2007), with changes in minimum temperature calculated according to Karl et al. (1993). Pereyra-Irujo et al. (2009) found almost identical results ($R^2 > 0.998$) by performing simulations using either weather data for individual years or average weather data for a 10-year period, with an earlier version of this model.

The model was run for the three sowing dates in the three locations, thus obtaining 9 sets of OA percentage values for each of the 13 genotypes. The ability of each of these 9 environments to predict the average performance of the genotypes (measured as the average OA percentage across all environments) was tested. Also combinations of two environments (locations or sowing dates) were tested. Then the same simulations were carried out using the estimated temperature data under the A1B scenario, and the ability of each environment or combination of them to predict the estimated average performance of the genotypes were tested. The ability of current environments to predict future performance was also tested.

2.6. Sensitivity analysis

A set of simulations were carried out in which different parameters of the OA percentage and phenology modules were individually changed in order to quantify their effect on the genotypic variability of OA percentage. Two genotypes were excluded from the analyses (ACA866 and Aromo 11) because the OA percentage relationship with temperature in the explored temperature range did not show the typical sigmoid shape (see Fig. 5 in the Section 3) and there could be inaccuracy in the estimation of their parameter values. For each of the parameters, one simulation was carried out in which the values for each genotype were replaced by the average of all genotypes. The results of each simulation (11 genotypes x three locations x three sowing dates) were compared to the results of the unmodified model, and the effect of the parameter change quantified as the root mean square error (RMSE) of OA percentage.

3. Results

3.1. Variability of fatty acid composition response to MNT

Differences both in mean values and stability across environments were found in OA percentage among the studied high oleic hybrids (Fig. 3A). General behavior of all high oleic hybrids plotted together showed that the OA percentage increased with MNT. This response could be described in general terms by a sigmoid function, in agreement with previous observations on traditional hybrids (Fig. 3B). A unique function, however, could not precisely describe the response of OA to MNT for all studied hybrids.

Oleic acid percentage was linearly and negatively related to linoleic acid percentage ($r^2 > 0.99$), while changes in saturated fatty acids with temperature were minor and with no clear trend with temperature changes (data not shown). Oleic acid varied between 68.9 and 94.4%, while linoleic acid content ranged between 0.8 and 20.4%.

Plots of OA percentage as a function of MNT for individual hybrids (Fig. 4) show sigmoid responses differing in their function parameters (maximal and minimum values, and amplitude). The sigmoid behavior was observed in 12 of the 17 analyzed hybrids. In 5 of them, minimum OA was not apparently attained, presumably because MNT in the sunflower growing region of Argentina is not low enough to reach their y_0 values. In those cases, the upper part of a sigmoid curve could still be detected (Fig. 5), and a constraint for

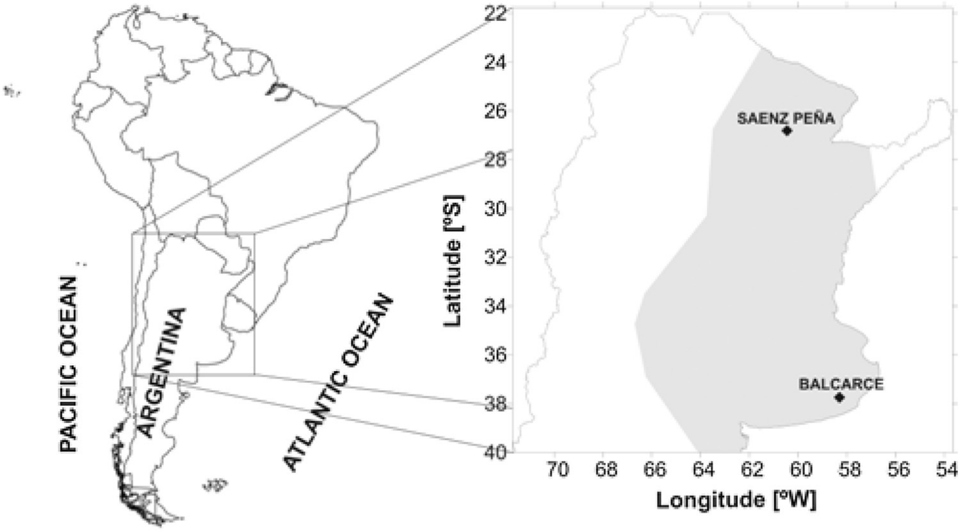

Fig. 2. Geographical position of selected locations in the sunflower producing region of Argentina (grey area).

the value of y_0 was considered for function fitting, based on results for complete curves was added ($70 < y_0 < 90$).

Diversity of responses of OA to temperature during grain filling was evidenced by analyzing the parameters of the model fitted to the data of each hybrid (Fig. 6).

The highest variability among the fitted parameters was found for b_{max}. Values for y_{max} were less variable than for y_0, therefore the range of variation in OA content was negatively correlated to y_0 value ($r^2 = 0.92$). On the other hand, b_{max} was not found to be correlated with any other parameter of the function. The temperature range of the 'high slope zone' (Fig. 1) was similar to that observed in traditional hybrids (9.4–23.8 °C, data not shown).

3.2. A meta-mechanism as a tool for identifying a low number of temperatures levels for

3.2.1. Phenotyping the response of oleic acid percentage to MNT

Genotypes that show the highest mean values of OA percentage and a low variability (hence higher stability) should be taken into account when breeding sunflower for high OA content. Analyzed hybrids were ordered according to their mean values of OA percentage, considering also their variability (Fig. 7). The ranking resulting from this analysis was obtained by using adjusted curves between 14.0 and 20.5 °C as detailed in Materials and Methods section.

Rankings obtained at individual temperatures or at different combinations between two or three temperatures were tested in order to determine whether a small set of experiments were able to reproduce the ranking obtained with the whole curve. For this, average values between OA content at one, two or three temperatures, were compared to the mean OA values obtained with the whole curve. The highest r^2 for one individual temperature was obtained at 19 °C ($r^2 = 0.837$). When considering mean OA at two or three temperatures, the best combinations were 15.5–20.0 °C and 15.5–17.5–20.5 °C according to their correlation values (0.969 and 0.993, respectively). This would allow predicting the position of each hybrid in the global ranking by knowing the value of OA percentage at the temperatures here reported.

3.3. Global warming projections and their effects on oleic acid percentages

Oleic acid percentage was simulated with a simple model for current (baseline) and A1B global warming scenarios, three different sowing dates and three locations with contrasting MNT. Current and expected mean temperature and mean minimum temperature in A1B scenario for the sunflower growing seasons are depicted in Table 2.

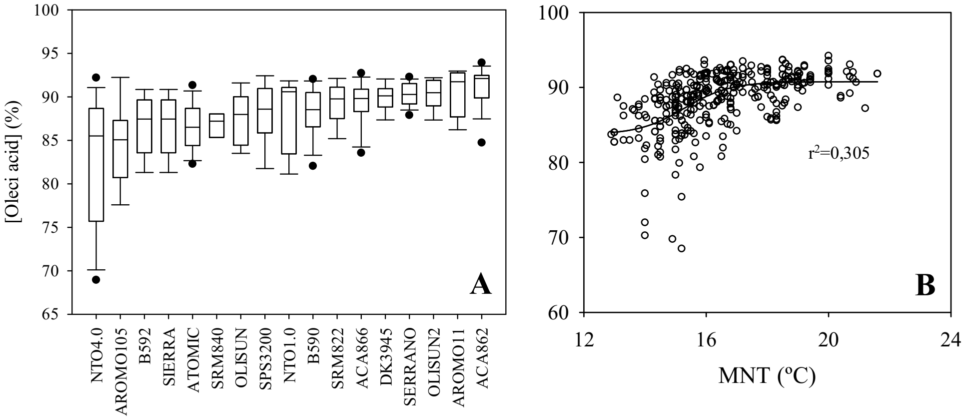

Fig. 3. (A) Boxplot of the oleic acid percentage of the different hybrids across environments. (B) Oleic acid percentage of 17 high oleic sunflower hybrids in the argentine sunflower growing region.

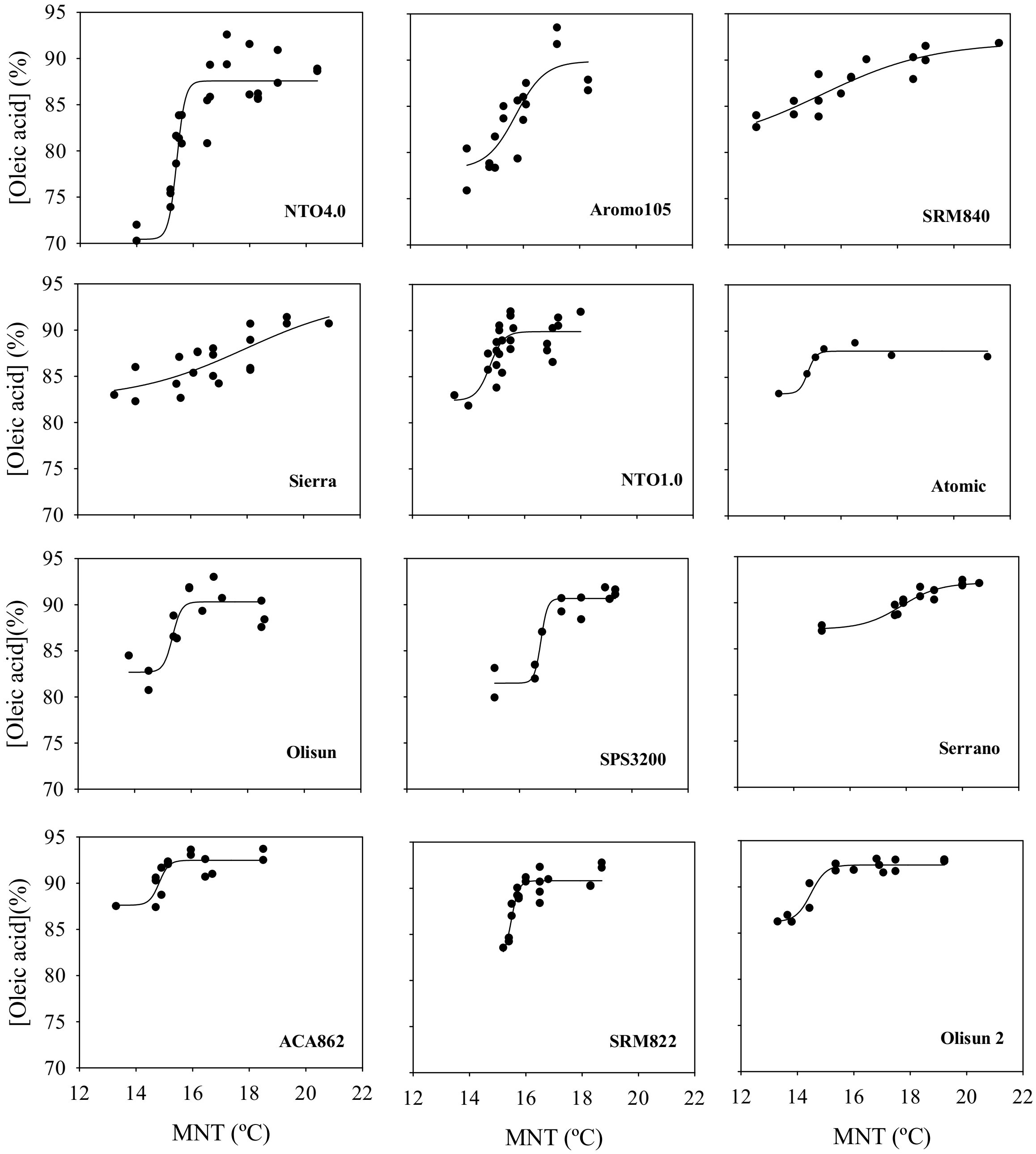

Fig. 4. Oleic acid percentage vs. MNT for the hybrids were the minimum oleic acid percentage (y_0) was attained. Dots represent experimental data. Continuous lines represent the sigmoid function (Eq. (1)) fitted to experimental data.

In baseline conditions, simulated data showed that 7–10 out of 13 genotypes reached y_{max} (at least 95% of the difference between y_0 and y_{max}) in Paraná and Sáenz Peña, but not at Balcarce. Under a global warming scenario, 8–10 out of 13 genotypes reach y_{max} values in Balcarce and 10–12 in Paraná and Sáenz Peña. (Table A1 in Appendix A).

The ability of the OA content in specific environments to predict the overall performance of genotypes under current environmental conditions was quantified as the R^2 of the correlation of the simulated OA percentages in one or in a combination of two environments against the simulated mean OA percentage across all environments (Table 3). High correlation values (>0.95) were obtained when combining data obtained in two locations: a southern one (Balcarce) and a northern one (Paraná or Sáenz Peña) at an intermediate sowing date.

Similarly the ability of the OA content in current environments to predict the future performance of genotypes under the A1B global warming scenario was quantified as the R^2 of the correlation of the simulated OA percentages in one or a combination of two current environments against the simulated mean OA percentage across all environments under the A1B scenario (Table 4). Higher correlation values between the simulated performance of genotypes under current and future environments were obtained only at warmer locations and at intermediate or late sowing dates (highlighted R^2 values in Table 4). Noteworthy, experiments performed in only one environment (i.e. Paraná or Sáenz Peña at a late sowing date) would be enough to evaluate the overall performance of genotypes under global warming conditions.

A sensitivity analysis was performed for parameters that define OA percentage in sunflower oil. Parameters considered were those

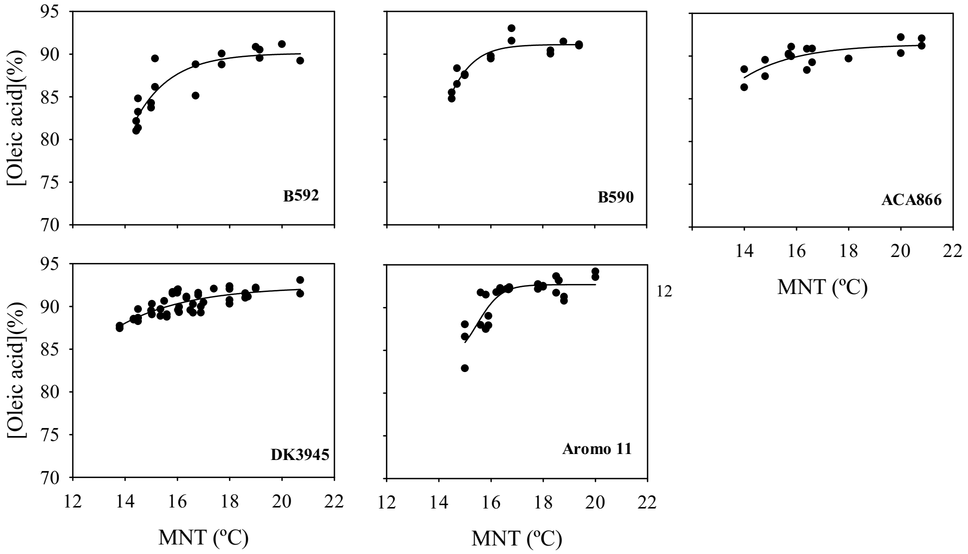

Fig. 5. Oleic acid percentage vs. MNT for the hybrids were the minimum oleic acid percentage (y_0) was not attained. Dots represent experimental data. Continuous lines represents the sigmoid function (Eq. (1)) fitted to experimental data.

included in the response function of OA percentage to temperature, and phenology parameters that would change the moment when the critical period for fatty acid composition is reached. Table 5 shows deviations from the OA percentage values of the original model (as RMSE values) as a consequence of replacing each genotype parameter by the mean parameter value for all genotypes. These deviations reflect the estimated effect of the genetic variability of each parameter on OA percentage. Results showed a null or low effect of phenology parameters in both current and future scenarios, but a significant effect of parameters defining OA percentage. Among the latter, the relative importance was different between current and future scenarios. Under current environmental conditions, changes in y_0 values showed the highest effect on OA percentage (over 2 percentage points), while the other parameters

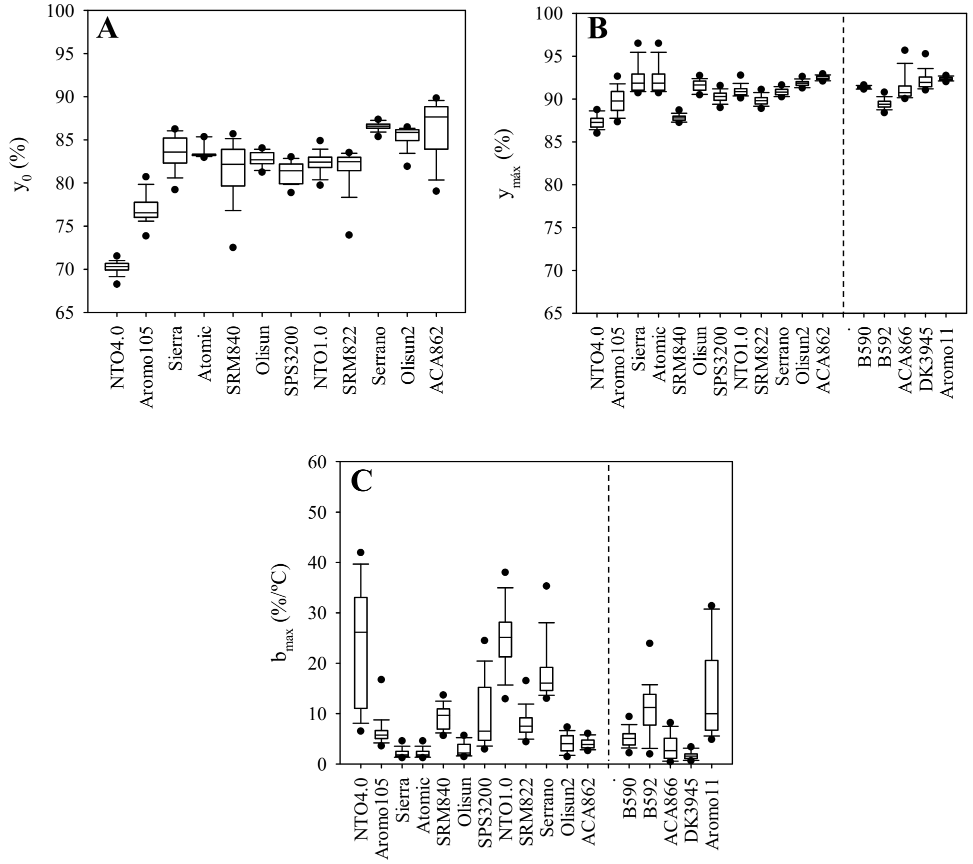

Fig. 6. Boxplot of parameters of Eq. (1) fitted to experimental data. y_{max} and b_{max} were calculated as in Izquierdo and Aguirrezábal (2008). Dashed line separates parameters obtained for complete curves (left side) from those of incomplete curves (right side).

Table 2
Mean (Mean T) and minimum night temperature (MNT) (°C) from sowing to flowering or during 100–300 °C day after flowering in the present (baseline) and in A1B scenario of global warming.

Location	Sowing date	Mean T sowing-flowering	Mean T sowing-flowering	Mean MNT 100–300	Mean MNT 100–300
		Baseline[a]	A1B[b]	Baseline[a]	A1B[c]
Balcarce	Early	15.5	17.1	13.4	16.5
	Inter	17.3	19.1	13.5	17.0
	Late	19.3	21.5	13.1	16.8
Paraná	Early	18.3	20.2	17.3	20.4
	Inter	20.3	22.5	18.3	21.9
	Late	23.3	25.9	19.1	23.4
Sáenz Peña	Early	17.9	20.1	15.8	19.2
	Inter	20.0	22.4	17.3	21.0
	Late	22.8	25.5	19.2	23.3

[a] Source: Servicio Meteorológico Nacional (Argentina).
[b] According to IPCC's emission scenario (Christensen et al., 2007).
[c] According to IPCC's emission scenario (Karl et al., 1993; Christensen et al., 2007).

Table 3
Correlation (R^2) of the simulated oleic acid percentages in one or in a combination of two environments against the simulated mean oleic acid percentage across all environments. Values shown in bold correspond to individual environments, while the remaining values are the combination of two locations and/or sowing dates. Highlighted R^2 values are those over 0.95.

		Balcarce			Paraná			Sáenz Peña		
Location	Sowing date	Early	Inter	Late	Early	Inter	Late	Early	Inter	Late
Balcarce	Early	**0.88**								
	Inter	0.88	**0.88**							
	Late	0.89	0.89	**0.89**						
Paraná	Early	0.98	0.98	0.98	**0.62**					
	Inter	0.96	0.96	0.96	0.73	**0.82**				
	Late	0.94	0.94	0.95	0.79	0.86	**0.88**			
Sáenz Peña	Early	0.91	0.91	0.91	0.51	0.57	0.60	**0.33**		
	Inter	0.98	0.98	0.98	0.61	0.72	0.78	0.51	**0.60**	
	Late	0.94	0.94	0.94	0.81	0.87	0.89	0.61	0.79	**0.89**

Table 4
Correlation (R^2) of simulated oleic acid percentages in one or in a combination of two current environments against the simulated mean oleic acid percentage across all environments under the A1B scenario. Values shown in bold correspond to individual environments, while the remaining values are the combination of two locations and/or sowing dates. Highlighted R^2 values are those over 0.95.

		Balcarce			Paraná			Sáenz Peña		
Location	Sowing date	Early	Inter	Late	Early	Inter	Late	Early	Inter	Late
Balcarce	Early	**0.66**								
	Inter	0.66	**0.66**							
	Late	0.67	0.67	**0.68**						
Paraná	Early	0.84	0.83	0.85	**0.76**					
	Inter	0.80	0.80	0.81	0.86	**0.93**				
	Late	0.78	0.78	0.79	0.91	0.95	**0.95**			
Sáenz Peña	Early	0.75	0.75	0.76	0.57	0.61	0.63	**0.34**		
	Inter	0.84	0.84	0.85	0.75	0.84	0.90	0.56	**0.73**	
	Late	0.77	0.77	0.78	0.92	0.96	0.96	0.64	0.91	**0.96**

showed an intermediate effect. These effects decreased under the A1B scenario for all parameter except for y_{max}, which showed the largest effect under these conditions.

4. Discussion

The achievement of a desired oil quality and the stability of fatty acid composition are important genetic improvement objectives in breeding programs of high oleic sunflower hybrids. Genetic variability for both mean OA percentage and stability was found among high oleic sunflower hybrids that are representative of those currently available in the Argentine seed market.

Response of OA percentage to MNT was studied by means of a well validated and robust equation previously established for traditional sunflower hybrids (Izquierdo and Aguirrezábal, 2008). When analyzing the response of all hybrids together to MNT, a sigmoid shape was observed. However, a unique function only explained a low proportion of the variation in OA content among the 17 hybrids here examined. In agreement with results obtained with traditional hybrids, when analyzing each hybrid individually, the sigmoid model accounted for the variation of OA percentage in all studied high oleic hybrids. Interestingly, in spite of the small difference between minimum and maximum OA percentage in high oleic hybrids, it was possible not only to establish relationships between OA and MNT, but also to characterize different responses among hybrids.

Genetic variability of the response of OA percentage to temperature was evidenced by the different parameters values obtained for different hybrids. The highest variability was found for b_{max}, followed by y_0, being y_{max} the less variable parameter, in agreement with results obtained for traditional hybrids (Izquierdo and Aguirrezábal, 2008). It is noteworthy that the range of variation of both b_{max} and y_0 among the studied high oleic hybrids was close to that found for traditional hybrids. Moreover, some high

Table 5
Deviations (shown as RMSE values) from the oleic acid percentage values of the unmodified model as a consequence of replacing each genotypic parameter by the mean parameter value for all genotypes, both under current environmental conditions and under the A1B global warming scenario. Highlighted values are those which show an effect larger than 1 percentage point.

	Oleic acid percentage parameters (Eq. (1))				Phenology parameters		
	y_0	y_{max}	x_0	B	Days to flowering (long photoperiod)	Days to flowering (short photoperiod)	Photoperiod effect
Current environmental conditions	2.6	1.2	1.3	1.1	0.0	0.1	0.1
A1B global warming Scenario	0.6	1.5	0.9	0.9	0.0	0.2	0.1

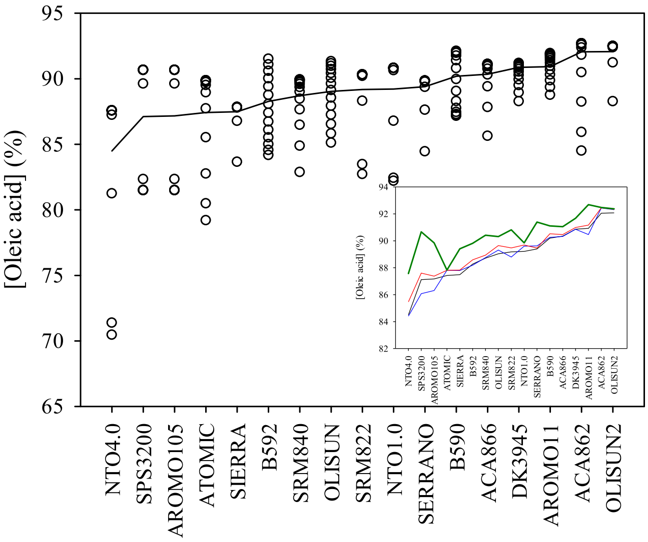

Fig. 7. Theoretical values of oleic acid percentage of the different hybrids. Hybrids were ordered according to the mean values of simulated data obtained by Eq. (1) from the lowest to the highest (continuous line). Symbols represent oleic acid percentage estimated at different temperatures every 0.5 °C between 14.0 and 20.5 °C. Inset: Continuous lines represent mean oleic acid percentage for: all data in the plot (black), oleic acid at 19.0 °C (green), 15.5–20.0 °C (blue); and 15.5–17.5–20.5 °C (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

oleic hybrids (i.e. NTO4.0 and NTO1.0) showed higher b_{max} than all the traditional hybrids studied by Izquierdo and Aguirrezábal (2008), revealing the strong response to temperature that can be found in some high oleic hybrids. The robustness of the applied model could aid in elucidating physiological processes underlying the responses to temperature in a complex biochemical pathway, such as fatty acids biosynthesis. For instance, the values of y_0 and y_{max} could reflect the maximum and minimum activity of the ODS enzyme, respectively, and b_{max} might be related to ODS sensitivity to temperature.

Genotypes studied in this work, as all commercial sunflower high oleic hybrids currently available in the seed market, carry the Pervenets high oleic mutation (Soldatov, 1976). Our data confirmed that the Pervenets mutation, that increases the average oleic acid percentage in the oil, did not eliminate the response of this quality trait to MNT. In agreement with this results, Alberio et al. (2016) found a similarly low but significant response to MNT in an inbred line carrying the Pervenets mutation, a high response in a non-mutated isoline (i.e. traditional sunflower), and a null response in an isoline with the mutation 29066 (León et al., 2013).

When growing high oleic sunflower, hybrids that can attain high OA percentage and that are stable across environments are highly desirable. Identifying high oleic hybrids with maximal high oleic percentage in traditional breeding programs is costly and time consuming. For this, plants must be grown under a wide range of temperatures during grain filling in order to generate a ranking and select those genotypes with higher mean values. In this work, a theoretical ranking was generated by fitting a sigmoid function for the response of OA to MNT of different hybrids and averaging data for each hybrid across many environments. Rankings were also obtained for individual temperatures or for combination of two or three temperatures and compared to the theoretical one. By doing so, it was possible to find a low number of effective environments to reproduce the rankings obtained with a wide range of temperatures. This information could facilitate the identification of the best high oleic genotypes by phenotyping high oleic percentage in a low number of experiments (e.g. in controlled or semi controlled conditions like growth chambers or greenhouses). Although phenotyping OA percentage in controlled or semi controlled conditions could be difficult at the first stages of the breeding process, where a high number of genotypes are frequently screened, it could be useful during the last stages to confirm the rankings of the selected genetic materials.

Sowing date and location are management practices that can be adopted to obtain oils with different composition (Pereyra-Irujo and Aguirrezábal, 2007). Simulations of OA percentage for different locations and sowing dates showed that maximum OA percentage (y_{max}) is not attained in 50% of the studied hybrids in some sowing dates at the warmest location here analyzed (Sáenz Peña). In spite of the temperature increase in a future global warming scenario, the maximum OA percentage may not be attained in 30% of the studied hybrids in the colder locations. These simulated results suggest that the stability of OA percentage could still be a concern in the future for high oleic hybrids breeding programs.

Simulations also helped to identify some combinations of locations x sowing dates where the global performance ranking is most likely to be reproduced. These environments could be useful for field phenotyping, especially in the first stages of the breeding process (see the precedent paragraph). In this work we found that in order to obtain a new variety with a high and stable OA content in any current environment, it would be necessary to select for high OA content in both cold and warm regions. On the other hand, under a global warming scenario and considering current cultivated sunflower hybrids, selection performed in warmer regions would be enough to select for the best genotypes. Methods used in this work to identify environments or combinations of environments for phenotyping in Argentina could be easily applied with the same goal for different regions of the world where sunflower is cultivated.

The sensitivity analysis shows that parameters involved in OA percentage response to temperature have largely more impact defining OA percentage in sunflower oil than phenology parameters, in both current and future scenarios. Moreover, the analysis allowed identifying the main avenues to improve the performance of high oleic hybrids. Nowadays, breeding strategies should aim at increasing y_0, the minimum OA percentage at low temperature, whereas in the future the increase in y_{max} should be the target.

Surprisingly, both in current and global warming scenarios, the effect of phenology parameters on OA percentage was null or low. These results disagree with literature based on empirical data or simulations that conclude that the effect of increased temperature on phenology would account for most changes in several plant traits due to clime variability or climate changes (e.g. Rezaei et al., 2015). This apparent contradiction could be partially explained by the fact that sunflower development and oil fatty acid composition depend on different temperature variables (mean and minimum night temperature, respectively). Climate models and regional global warming projections estimate not only an increase in mean temperature but also in the likelihood of an asymmetric change in temperature. In this sense, night-time minimum increases more rapidly than the day-time maximum, a phenomenon that has been observed during the last decades (Rusticucci and Barrucand, 2004). In addition, the low difference between y_0 and y_{max} found in most of the studied high oleic sunflower hybrids together with the steep response to temperature (e.g. in comparison to traditional hybrids) could partially explain the low effect of plant development under current and global warming scenarios.

5. Conclusion

In this work, the genetic variability of OA percentage of high oleic hybrids of sunflower in response to temperature was assessed by using a meta-mechanism previously proposed and widely validated. Based also on this equation, we could identify the best temperatures for fatty acid composition phenotyping in controlled conditions, and also the best environments for phenotyping in the field, both in current and future scenarios. Simulations suggest that the stability of OA percentage could still be a concern even under a global warming scenario. Considering the results obtained in this work, the main avenues for genetic improvement of OA percentage in current breeding programs should be to aim for increasing the minimum OA percentage, whereas in a future global warming scenario, the interest should be moved towards increasing the maximum attainable OA percentage.

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Appendix A.

Table A1
Oleic acid percentage simulated according to Pereyra-Irujo and Aguirrezábal (2007) for the present (baseline) and under global warming A1B scenario.

Scenario	BASELINE	BASELINE	BASELINE	BASELINE	BASELINE	BASELINE	BASELINE	BASELINE	BASELINE	A1B	A1B	A1B	A1B	A1B	A1B	A1B	A1B	A1B
Location	BALCARCE	BALCARCE	BALCARCE	PARANA	PARANA	PARANA	SÁENZPEÑA	SÁENZPEÑA	SÁENZPEÑA	BALCARCE	BALCARCE	BALCARCE	PARANA	PARANA	PARANA	SÁENZPEÑA	SÁENZPEÑA	SÁENZPEÑA
Sowing date	EARLY	INTER	LATE	EARLY	INTER	LATE	EARLY	INTER	LATE	EARLY	INTER	LATE	EARLY	INTER	LATE	EARLY	INTER	LATE
OLISUN2	86.7	86.6	86.2	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4	92.4
ACA862	87.6	87.6	87.6	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5	92.5
AROMO11	83.8	83.8	83.6	92.6	92.7	92.7	91.1	92.6	92.7	92.3	92.5	92.3	92.7	92.7	92.7	92.7	92.7	92.7
ACA866	87.3	87.3	86.3	90.8	91.0	91.1	90.0	90.7	91.1	90.5	90.6	90.5	91.2	91.3	91.3	91.1	91.2	91.3
SERRANO	87.1	87.1	87.1	89.1	90.7	91.6	87.4	88.9	91.7	87.9	88.6	88.2	92.1	92.2	92.2	91.6	92.1	92.2
NTO1.0	82.6	82.6	82.4	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8	89.8
SRM822	82.2	82.2	82.2	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8	90.8
OLISUN	82.7	82.7	82.7	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3	90.3
SRM840	84.1	84.2	83.4	89.8	90.3	90.6	88.2	89.7	90.8	88.9	88.9	88.4	91.5	91.6	91.8	91.1	91.5	91.8
SIERRA	83.8	83.7	83.4	87.7	88.9	89.7	85.6	87.5	90.0	86.6	87.2	86.5	91.4	92.3	92.8	90.1	91.8	92.8
SPS3200	81.5	81.5	81.5	90.7	90.7	90.7	81.5	90.7	90.7	87.0	90.6	88.7	90.7	90.7	90.7	90.7	90.7	90.7
NTO4.0	70.3	70.3	70.3	87.5	87.5	87.5	87.3	87.5	87.5	87.5	87.5	87.5	87.5	87.5	87.5	87.5	87.5	87.5

References

Aguirrezábal, L.A.N., Izquierdo, N.G., Nolasco, S.M., Dosio, G.A., 2001. Manual Práctico Para Cultivo De Girasol. In: Díaz Zorita, M., Duarte, G. (Eds.). Hemisferio Sur, Buenos Aires, Argentina.

Aguirrezábal, L., Martre, P., Pereyra-Irujo, G., Echarte, M., Izquierdo, N., 2014. Improving grain quality: ecophysiological and modeling tools to develop management and breeding strategies. In: Sadras, V., Calderini, D. (Eds.), Crop Physiology. Applications for Genetic Improvement and Agronomy. Academic Press, London, pp. 423–465.

Alberio, C., Izquierdo, N.G., Galella, T., Zuil, S., Reid, R., Zambelli, A., Aguirrezábal, L., 2016. A new sunflower high oleic mutation confers stable oil grain fatty acid composition across environments. Eur. J. Agron. 73, 25–33.

Burke, J.M., Knapp, S.J., Rieseberg, L.H., 2005. Genetic consequences of selection during the evolution of cultivated sunflower. Genetics 171, 1933–1940.

Chmielewski, F.-M., Rötzer, T., 2001. Response of tree phenology to climate change across Europe. Agric. Forest Meteorol. 108, 101–112.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A., Whetton, P., 2007. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.). Cambridge University Press, Cambridge, UK and New York, USA.

Fernández-Martínez, J., Jimenez, A., Dominguez, J., Garcia, J.M., Garces, R., Mancha, M., 1989. Genetic analysis of the high oleic acid content in cultivated sunflower (*Helianthus annuus* L.). Euphytica 41, 39–51.

Haddadi, P., Yazdi-Samadi, B., Langlade, N.B., Naghavi, M.R., Berger, M., Kalantari, A., Calmon, A., Maury, P., Vincourt, P., Sarrafi, A., 2013. Genetic control of protein: oil and fatty acids content under partial drought stress and late sowing conditions in sunflower (*Helianthus annuus*). Afr. J. Biotechnol. 9, 6768–6782.

Hall, A.J., Richards, R.A., 2013. Prognosis for genetic improvement of yield potential and water limited yield of major grain crops. Field Crops Res. 143, 18–33.

Hall, A.J., Feoli, C., Ingaramo, J., Balzarini, M., 2013. Gaps between farmer and attainable yields across rainfed sunflower growing regions of Argentina. Field Crops Res. 143, 119–129.

Hammer, G., Cooper, M., Tardieu, F., Welch, S., Walsh, B., van Eeuwijk, F., Chapman, S., Podlich, D., 2006. Models for navigating biological complexity in breeding improved crop plants. Trends Plant Sci. 11, 587–593.

Izquierdo, N.G., Aguirrezábal, L.A.N., 2008. Genetic variability in the response of fatty acid composition to minimum night temperature during grain filling in sunflower. Field Crops Res. 106, 116–125.

Izquierdo, N.G., Aguirrezábal, L.A.N., Andrade, F.H., Pereyra, V., 2002. Night temperature affects fatty acid composition in sunflower oil depending on the hybrid and the phenological stage. Field Crops Res. 77, 115–126.

Izquierdo, N.G., Aguirrezábal, L.A.N., Andrade, F.H., Cantarero, M.G., 2006. Modeling the response of fatty acid composition to temperature in a traditional sunflower hybrid. Agron. J. 98, 451–461.

Jones, H.G., 2014. Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology, 3rd edition. Cambridge University Press, ISBN 978-0-521-27959-8.

Karl, T.R., Knight, R.W., Gallo, K.P., Peterson, T.C., Jones, P.D., Kukla, G., Plummer, N., Razuvayev, V., Lindseay, J., Charlston, R.J., 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. Bull. Am. Meteorol. Soc. 74, 1007–1023.

Labalette, F., Jouffret, P., Merrien, A., 2012. Oleic Sunflower production: current situation and trends for the future, Proceedings of 18th International Sunflower Conference.

Lacombe, S., Bervillé, A., 2000. Analysis of desaturase transcript accumulation in normal and high oleic oil in sunflower development seeds. In: Proceedings of the 15th International Sunflower Conference, Toulouse, France, pp. 1–6.

Lagravère, T., Kleiber, D., Dayde, J., 1998. Conduites culturales et performances agronomiques du tournesol oléique: réalités et perspectives. Ocl-Ol. Corps Gras Li. 5, 477–485.

León, A.J., Zambelli, A.D., Reid, R.J., Morata, M.M., Kaspar, M., 2013. Nucleotide sequencesmutated by insertion that encode a truncated oleate desaturase protein, proteins, methods and uses. Patent WO 2013/004281 A1, January 10, 2013.

Luquez, J.E., Aguirrezábal, L.A.N., Agüero, M.E., Pereyra, V.R., 2002. Stability and adaptability of cultivars in nonbalanced yield trials. Comparison of methods for selecting 'high oleic' sunflower hybrids for grain yield and quality. J. Agron. Crop Sci. 188, 225–234.

Parent, B., Tardieu, F., 2012. Temperature responses of developmental processes have not been affected by breeding in different ecological areas for 17 crop species. New Phytol. 194, 760–774.

Parton, W., Logan, J., 1981. A model for diurnal variation in soil and air temperature. Agric. Meteorol. 23, 205–216.

Pereyra-Irujo, G.A., Aguirrezábal, L.A.N., 2007. Sunflower yield and oil quality interactions and variability: analysis through a simple simulation model. Agric. Forest Meteorol. 143, 252–265.

Pereyra-Irujo, G.A., Izquierdo, N.G., Covi, M., Nolasco, S.M., Quiroz, F., Aguirrezábal, L.A.N., 2009. Variability in sunflower oil quality for biodiesel production: a simulation study. Biomass Bioenergy 33, 459–468.

Putt, D.E., 1997. Early history of sunflower. In: Schneiter, A.A. (Ed.), Sunflower Technology and Production. American Society of Agronomy/Crop Science Society of America/Soil Science Society of America, Wisconsin, USA, pp. 1–19.

Rezaei, E.E., Siebert, S., Ewert, F., 2015. Intensity of heat stress in winter wheat phenology compensates for the adverse effect of global warming. Environ. Res. Lett. 10 (2), 024012.

Roche, J., Bouniols, A., Mouloungui, Z., Barranco, T., Cerny, M., 2006. Management of environmental crop conditions to produce useful sunflower oil components. Eur. J. Lipid Sci. Technol. 108, 287–297.

Rusticucci, M., Barrucand, M., 2004. Observed trends and changes in temperature extremes over Argentina. J. Climate 17, 4099–4107.

Sadras, V.O., Monzon, J.P., 2006. Modelled wheat phenology captures rising temperature trends: shortened time to flowering and maturity in Australia and Argentina. Field Crops Res. 99, 136–146.

Schneiter, A.A., Miller, J.F., 1981. Description of sunflower growth stages. Crop Sci. 21, 901–903.

Soldatov, K.I., 1976. Chemical mutagenesis in sunflower breedings. In: Proceedings of the 7th International Sunflower Conference, Krasnodar, USSR, pp. 352–357.

Sukhija, P.S., Palmquist, D.L., 1988. Rapid method for determination of total fatty acid content and composition of feedstuffs and feces. J. Agric. Food Chem. 36, 1202–1206.

Tardieu, F., 2003. Virtual plants: modeling as a tool for the genomics of tolerance to water deficit. Trends Plant Sci. 8, 9–14.

Triboï-Blondel, A.M., Bonnemoy, B., Falcimagne, R., Martignac, M., Messaoud, J., Philippon, J., Vear, F., 2000. The effect of temperature from flowering to maturity on seed composition of high oleic sunflower inbreeds and mid oleic hybrids. In: Proceedings of the 15th International Sunflower Conference, Toulouse, France, pp. 67–72.