



Adaptation assessment of drought tolerance in maize populations from the Sahara in both shores of the Mediterranean Sea

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Abstract Drought is the main stress for agriculture, and maize (*Zea mays* L.) germplasm from the Sahara has been identified as potential source of drought tolerance; however, information about adaptation of semitropical maize germplasm from the Sahara to temperate areas has not been reported. Our objective was assessing the adaptation of maize germplasm from Saharan oases as sources of drought tolerance for improving yield and biomass production under drought conditions in temperate environments. A collection of maize populations from Saharan oases was evaluated under drought and control conditions in Spain and Algeria. Algerian populations were significantly different under drought for most traits, and the significant genotype × environment interactions indicated that drought tolerance is genotype-dependent, but tolerance differences among genotypes change across environments. Based on yield, the Algerian maize populations PI527474, PI527478, PI527472, PI527467, PI527470, and PI527473 would be appropriate sources of drought tolerance for temperate environments. Concerning biomass production, the most interesting populations were PI527467,

PI542685, PI527478, and PI527472. These Saharan populations could provide favorable alleles for drought tolerance for temperate breeding programs, and could also be used for studying mechanisms and genetic regulation of drought tolerance.

Keywords *Zea mays* L. · drought stress · seedling growth · Algerian landraces

Introduction

Drought is the main challenge for maize production worldwide (Rojas et al. 2011; Fisher et al. 2015), and causes yield losses of around 20 % (Chen et al. 2012). Furthermore, drought is expected to worsen with climate change (Betrán et al. 2003; Witt et al. 2012). Identification of sources of drought tolerance is of paramount importance for designing plant breeding programs for improving drought tolerance. Consequently, the International Maize and Wheat Improvement Center (CIMMYT) has evaluated maize accessions from tropical areas (Flint-Garcia et al. 2005; Chen et al. 2012). Several authors have evaluated temperate populations for drought tolerance in Mediterranean areas with limited success (Djemel et al. 2018; Gouesnard et al. 2016; Hallauer et al. 2010). A more promising strategy consist on incorporating maize populations from desserts into breeding programs under temperate conditions.

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Maize from the desert provides diverse mechanisms of drought tolerance for plant survival under extreme stress conditions (Djemel et al. 2017). Populations from the Algerian Sahara can be potential sources of favorable alleles for drought tolerance that can be incorporated into elite temperate varieties. Djemel et al. (2019) evaluated a collection of 18 maize populations from Saharan oases under simulated drought conditions and in the field, and identified drought tolerant populations based on germination, root development, yield, and water use efficiency (WUE). They concluded that populations show diverse mechanisms for drought tolerance potentially useful for maize breeding programs.

Several authors have assessed the genetic diversity of maize populations collected in the Algerian oases, which are characterized by extreme temperature and aridity (Rahel-Bouziane and Feliachi 2006; Djemel et al. 2012; Aci et al. 2013; Djemel et al. 2017). Algerian maize germplasm contains high phenotypic and genetic diversity and wide adaptation to temperate regions (Djemel et al. 2012; Aci et al. 2013). Moreover, Cherchali et al. (2018) identified heterotic patterns among Algerian maize populations and between them and heterotic groups from northern and southern Spain and US Corn Belt Dent.

Our objective was assessing adaptation of maize germplasm from Saharan oases as sources of drought tolerance for improving yield and biomass production under drought conditions in temperate environments of both shores of the Mediterranean Sea.

Materials and methods

Plant material

The Eighteen open-pollinated Algerian maize populations were provided by the North Central Regional Plant Introduction Station (USA) These populations collected from diverse Algerian locations throughout the Sahara were evaluated along with EPS14(FR)C3, a maize composite that represents maize from the dry Spain, EPS13(FR)C3, from the humid Spain, and two hybrids representing the US Dent \times European Flint heterotic pattern (A239 \times EP74 and A638 \times EP56).

Experimental design

The 22 varieties were assayed under drought and control conditions, following a split-plot design with three replications, in 2016 and 2017 in Alger and northwestern Spain. The experimental plot consisted of two rows with 30 kernels per row and one kernel per hill. The rows were spaced 0.80 m apart, and the hills were spaced 0.20 m apart to obtain a final density of 60,000 plants ha^{-1} . Appropriate techniques for cultivation were carried out according to local practices. Harvest and weed control were done manually.

In Algiers (36° 47' N, 2° 03' E, altitude 32 m a.s.l.), the field trials were sown on 26th of April and 27th of April, in 2016 and 2017, respectively. Maize under control and drought conditions received 600 and 200 mm from sowing to post-flowering, respectively. Irrigation was applied once a week to reach the total amount of water not provided by rainfall. In northwestern Spain, a trial was sown under control conditions at Pontevedra (Latitude 42.40° N and Longitude 8.63° W) on the 4th of May of 2016, and trials under control and drought conditions were sown on the 23rd of May of 2017 in Xinzo de Limia (Latitude 42.07° N and Longitude 7.73° W). No irrigation was applied to the trial under drought stress in Xinzo de Limia.

Data collection

Data collected in each plot were: early vigor (Scale 1–9: 1 = weak plant to 9 = strong plant), days to anthesis (from planting to 50 %plants with anthers), days to silking (from planting to 50% plants silking), ASI (difference between days to silking and days to anthesis), plant height (PH, of 10 plants: from the soil to the top of the tassel), ears per plant (EarsPP), grain yield [weight of grain per hectare at 140 g kg^{-1} moisture in t (Mg ha^{-1})], grain moisture (percentage of water in grain at harvest), stover moisture (percentage of water calculated on ten plants without ears), and dry stover yield (computed by multiplying the total weight, in grams, of ten plants without ears by the stover moisture and refereed as Mg ha^{-1}).

Statistical analyses

Analyses of variance were performed for each trait, the sources of variation being environments (year \times location was considered as one environment),

treatments (well-watered and drought stress), genotypes, repetitions and their interactions. Treatments and populations were considered fixed effects; while any other effect or interaction was considered random. Mean comparisons were made with the Fisher's protected LSD at $p \leq 0.05$. All analyses were carried out with the statistical program SAS (2008).

Results

Environmental conditions

Algiers is in a sub humid region of the north of Algeria with 690 mm of annual rainfall. The driest months were May, June, July and August with an average of 36 mm, 14 mm, 2 mm and 4 mm of precipitation, respectively. Monthly rainfall in 2016 in Pontevedra was 183.8 mm in May, 60.9 in June, 7.3 in July, 23.9 in August, 91.1 in September and 100.0 in October. Therefore, these populations could not be evaluated for drought tolerance in Pontevedra in 2016. In order to evaluate these populations under drought conditions in northwestern Spain, field trials in 2017 field trials were located in Xinzo de Limia, where monthly rainfall was 78.5 in May, 44.8 in June, 25.8 in July, 29.1 in August, 0.3 in September and 10.6 in October. During the maize growing season (April to October), mean temperatures in Pontevedra were from 15.8 to 21.4 °C, minimum temperatures were between 1 and 16.4 °C, and maximum temperatures were between 23.8 and 28.2 °C, while in Xinzo de Limia mean temperatures were between 12.3 and 19.6 °C, minimum temperatures were between 2.4 and 11.1 °C and maximum temperatures were between 21.8 and 29.7 °C.

Analyses of variance

Differences among maize varieties were significant for all traits, and the variety \times treatment interaction was significant for all traits except emergence and grain moisture (data not shown). The genotype \times environment interaction was significant for most traits and was often due to genotype rank changes across environments; therefore, we report these analyses individually for drought conditions in northwestern Spain, although in northwestern Spain in 2016 only the

control environment was carried out due to the abundant rainfall.

Vegetative traits

The means of the genotypes under control and drought conditions across locations show the average drought tolerance of the varieties, while the mean values under drought conditions in Pontevedra show the potential value of those genotypes for Spain. Mean germination was not significantly affected by drought and several Algerian populations had similar or higher germination than the temperate varieties under drought conditions (Table 1). Average early vigor was reduced under drought conditions compared to the control treatment. Some Algerian populations had high early vigor (especially PI527467 and PI527474) under drought conditions in Spain and across environments, while the lowest vigor values were also found among Algerian populations.

As expected, the effects of drought stress were more evident at adult plant stages; actually, differences between treatments (control and drought) were significant for all adult traits. Some of these tropical and subtropical populations were not able to flower under the drought conditions of northern Spain because their photoperiod sensitivity delayed growth and plants were exposed to drought stress at earlier stages of development (Table 1). Drought stress at early stages of development and lack of adaptation can explain that five Algerian populations did not reach male flowering while one did not reach female flowering. Populations with the latest flowering were from southern Algeria, while populations with the earliest flowering came from all origins. As expected, mean pollen shedding was delayed under drought conditions; however, differences between control and drought for mean silking were not significant. The earliest population in all conditions was PI527476, though, under drought conditions in Spain, it was not significantly different from A638 \times EP56 and PI527469. The earliest population had also a negative ASI under drought in Spain. On the other side, in Spain, female flowering of the populations PI527477, PI542683 and PI542687 was considerably delayed under drought compared to control conditions and that contributed to the high ASI values for those populations, probably caused by photoperiod sensitivity rather than by drought susceptibility. Differences

Table 1 Mean comparison for vegetative traits among Algerian maize populations evaluated in Algeria and Spain in 2016 and 2017 under control and drought conditions

Population	Emergence (%)		Early vigor (1-9) ^a		Days to pollen (days)		Days to silking (days)			
	Control Spain	Drought Spain	Control combined	Drought combined	Control combined	Drought combined	Control combined	Drought combined		
									Spain	Spain
EPS13FRC3	56.3	55.3	7.3	5.8	65.5	64.8	67.2	67.3	69.0	
EPS14FRC3	53.8	52.3	6.8	5.7	65.1	63.2	66.3	69.3	79.0	
A239 × EP74	48.7	37.7	7.2	6.3	66.7	66.0	67.6	73.2	82.7	
A638 × EP56	60.3	60.3	7.3	5.9	62.9	64.2	64.0	69.0	69.0	
PI527464	52.0	55.3	5.5	4.2	73.5	67.0	74.3	69.0		
PI527465	60.3	58.3	6.3	4.9	64.8	63.7	66.8	69.4	76.0	
PI527467	61.2	60.3	6.8	5.8	67.3	68.4	69.5	68.4		
PI527469	63.0	58.7	6.3	4.7	64.7	64.6	65.7	67.4	71.5	
PI527470	50.7	52.3	5.3	5.2	66.4	68.0	66.2	68.1	74.3	
PI527472	61.8	61.3	6.7	5.2	65.8	64.6	67.6	68.4	73.0	
PI527473	58.0	60.3	6.0	5.9	64.6	62.4	65.3	66.4	75.0	
PI527474	59.0	61.7	6.2	5.4	65.6	62.3	66.9	67.1	77.0	
PI527475	55.5	57.3	5.4	5.6	65.3	62.7	65.7	66.1	70.7	
PI527476	36.8	25.0	4.5	4.9	59.8	57.3	58.8	55.5	55.3	
PI527477	57.2	53.3	5.9	4.6	71.8	72.4	75.5	75.9	104.0	
PI527478	54.7	53.3	6.0	5.6	61.4	61.3	62.3	64.0	68.0	
PI542683	51.8	55.0	5.8	5.2	71.4	70.8	72.3	73.4	104.0	
PI542684	56.2	57.3	7.1	5.4	82.7	72.5	82.3	70.7		
PI542685	51.8	58.0	6.3	5.0	80.6	71.5	80.6	68.0		
PI542687	49.7	53.7	5.3	4.3	74.8	73.7	76.8	82.0	104.0	
PI542688	51.5	55.3	5.7	4.7	69.8	63.3	71.7	68.0		
PI542689	57.7	56.7	5.6	4.9	70.3	69.1	71.3	73.1	86.5	
LSD (0.05)	4.9	7.2		0.78	1.9	2.4	1.8	4.7	17.2	
Mean	54.9	54.5	6.1	5.2	68.2	65.9	69	68.9		
Population	ASI (days) ^c		Plant height (cm)		Ear height (cm)		Ears per plant (N.)			
	Control Combined	Drought Combined	Control Spain	Drought Spain	Control combined	Drought combined	Control combined	Drought combined		
									Spain	Spain
EPS13FRC3	1.7	5.7	4.0	204.4	147.6	180.4	89.1	1.34	0.79	0.26

Table 1 continued

Population	ASI (days) ^c		Plant height (cm)		Ear height (cm)		Ears per plant (N.)	
	Control Combined	Drought Spain	Control combined	Drought Spain	Control combined	Drought Spain	Control combined	Drought Spain
EPS14FRC3	1.2	6.1	205.4	164.8	100.2	83.3	1.40	0.94
A239 × EP74	0.9	7.2	202.9	158.5	89.4	79.8	1.12	0.89
A638 × EP56	1.1	5.1	194.4	158.2	79.4	70.3	1.10	0.87
PI527464	1.1	2.0	151.9	109.6	63.6	41.2	1.35	0.93
PI527465	1.5	6.4	167.8	131.2	68.6	56.8	1.68	0.84
PI527467	1.4	4.6	190.9	137.7	90.6	75.5	1.28	0.65
PI527469	1.0	4.6	179.4	123.7	85.8	67.5	1.66	0.84
PI527470	0.4	3.2	172.2	133.3	79.9	67.5	1.69	1.08
PI527472	1.8	6.0	190.3	149.3	78.3	67.2	1.32	0.96
PI527473	1.2	4.8	178.7	163.0	76.3	73.4	1.54	1.04
PI527474	1.7	4.8	190.5	151.3	88.4	83.9	1.76	1.07
PI527475	0.7	3.4	181.6	155.8	84.1	86.1	1.74	0.99
PI527476	1.0	0.1	133.6	125.4	40.9	45.9	1.28	0.87
PI527477	2.7	7.0	194.5	134.5	101.6	71.6	1.30	0.83
PI527478	1.2	2.7	169.3	152.9	65.9	69.4	1.61	0.93
PI542683	1.1	4.7	193.4	143.9	105.4	78.0	1.38	0.86
PI542684	4.1	3.0	216.3	152.6	130.6	93.4	1.08	0.86
PI542685	3.6	2.7	234.4	156.6	140.3	93.6	1.15	0.91
PI542687	1.9	9.6	179.9	132.6	94.8	65.0	1.32	0.92
PI542688	1.5	4.8	174.5	131.3	82.7	62.4	1.47	0.71
PI542689	1.2	5.7	177.0	136.0	90.0	67.0	1.32	0.59
LSD 0.05	1.5	4.1	10.8	18.5	7.2	11.0	0.31	0.41
Mean	1.38 b	4.81 a	185.6 a	141.3 b	87.5 a	71.6 b	1.41 a	0.88 b

For each trait, mean values under drought in Spain are presented in the third column

^a Early vigor was recorded following a scale from 1 = weak plant to 9 = strong plant

^b Emergence data were not recorded in Algeria

^c ASI means Anthesis – silking interval

between populations were not significant for ASI under drought in Spain, but the mean ASI under drought was significantly higher under stress than under control conditions, as expected. Interestingly enough, some populations improved their ranks for some traits under drought conditions respect to their ranks under control conditions, particularly PI542684 and PI542685 had the largest ASI under control and the shortest ones under drought.

Mean plant height was significantly reduced under drought conditions, compared with control conditions (Table 1). Temperate varieties had medium plant height under control, but they had the tallest plants under drought conditions, particularly in Spain, and this was also true for the Algerian populations PI527474, PI527475, PI527478, and PI542684, indicating that they were either drought tolerant or they had fair adaptation. Contrarily, the populations PI527464 and PI542687 had much shorter plants under drought than under control conditions, and they had the shortest plants under drought in Spain. Ear height followed similar patterns to plant height, though both temperate hybrids had medium ear height in all environments.

Prolificacy is a clear indicator of drought tolerance but differences among populations were not significant under drought conditions and genotype ranks for the number of ears per plant were similar under control and drought conditions in Spain. However, in Spain, PI542688 was among the populations with the lowest prolificacy under control conditions; while presented the highest prolificacy under drought; conversely, EPS14FRC3, PI527465 and PI542688 had medium prolificacy under control and low values under drought.

Grain and stover yields and moistures

Mean grain yield was significantly reduced under drought except for PI527476, although this population had no yield under drought in Spain (Table 2). Even though populations were not significantly different for grain yield under drought in Spain, eight Algerian populations and EPS14FRC3 were not able to produce grain in that environment. PI527470, PI527473, PI527474, PI527472, and PI542683 had medium yield under drought conditions, were among those with the highest yield values under control conditions, and were able to produce grain under drought in Spain.

Stover yields and stover moisture were only recorded in Xinzo de Limia and both traits were significantly reduced by drought. The populations that improved their ranks for stover yield under drought conditions compared to control conditions were PI527467 and PI527472, while PI542685 had high stover yield under control and drought conditions. For biomass moisture, the populations that had more favorable ranks under drought compared to control conditions, were PI527474, PI527475, and PI527478.

Discussion

Maize populations from the Algerian Sahara were evaluated under water stress to identify populations that were adapted to both shores of the Mediterranean Sea and, therefore, could be used as potential sources of drought tolerance in temperate breeding programs. We found large genetic diversity within this group of populations, as well as significant genotype \times environment interactions, as expected, given that these populations have a large diversity in geographical adaptation. The large phenotypic and genotypic diversity of Algerian maize populations has been previously reported by Aci et al. (2013).

The potential value of Algerian germplasm has been previously reported with other populations from the same area (Djemel et al. 2012, 2017, 2019). EPS14(FR)C3 and EPS13(FR)C3 represent the germplasm adapted to the Mediterranean area and the Atlantic coast of Spain, respectively, and the US Dent \times European Flint hybrids (A239 \times EP74 and A638 \times EP56) belong to the most common group of germplasm grown in Europe. Concerning the Algerian populations, PI542684 and PI542685 come from the tropical south of Algeria, and the other populations come from the temperate area of the Sahara.

The populations PI542684 and PI542685 were not able to flower under drought conditions in northwestern Spain because their vegetative stage was extended and made them especially sensitive to water stress, although they produced viable grain under control conditions. The current data show an interaction between drought tolerance and adaptation, i.e. as plant growth advanced, the effects of water stress increased. Consequently, genotypes were not significantly different at germination, while yield was severely affected for those populations with the highest drought

Table 2 Mean 1 comparison for yield and moisture among Algerian maize populations evaluated in Algeria and Spain in 2016 and 2017 under control and drought conditions

Population	Grain yield (Mg ha ⁻¹) 14 % moisture			Grain moisture (%)			Dry biomass (Mg ha ⁻¹)		Biomass moisture (%)	
	Control Combined	Drought combined	Drought Spain	Control combined	Drought combined	Drought Spain	Control Spain	Drought Spain	Control Spain	Drought Spain
EPS13FRC3	4.70	0.85	1.24	16.9	12.6	18.4	4.55	3.89	48.4	26.0
EPS14FRC3	3.66	0.99		18.6	11.0		5.35	3.87	51.3	27.0
A239 × EP74	6.02	2.00	1.80	17.1	12.9	18.6	8.18	5.11	52.7	28.1
A638 × EP56	5.89	1.16	1.57	12.8	12.6	18.6	4.64	3.32	62.1	35.4
PI527464	3.50	1.10		18.6	10.0		4.25	2.04	52.2	30.8
PI527465	4.06	1.02	0.61	16.2	11.4	20.5	4.00	2.46	47.1	29.6
PI527467	4.95	0.97		18.9	9.7		5.96	4.12	43.4	26.5
PI527469	3.33	1.12	2.53	15.1	12.2	20.1	5.22	3.59	61.1	37.7
PI527470	3.62	1.36	2.04	14.4	10.8	16.8	4.60	2.75	57.3	31.6
PI527472	4.45	1.24	0.86	15.6	12.2	19.6	5.65	3.91	50.3	29.7
PI527473	3.82	1.93	1.45	13.9	11.6	14.0	4.80	3.23	59.9	29.7
PI527474	3.75	1.60	1.21	15.6	10.7	16.4	4.36	2.57	66.6	33.4
PI527475	2.88	1.60		14.5	10.0		4.15	2.72	67.9	37.2
PI527476	1.40	1.32		13.0	8.8		1.66	2.54	69.1	69.5
PI527477	2.80	0.87	1.53	17.8	12.9	22.1	4.45	3.55	43.1	26.8
PI527478	2.57	1.17		11.7	7.4		3.28	2.35	69.8	46.8
PI542683	4.26	1.59	0.81	16.0	12.2	19.4	5.35	3.50	46.3	25.0
PI542684	2.05	1.00	0.99	22.4	21.0	31.9	10.19	3.99	29.7	21.1
PI542685	4.95	0.65		23.4	11.9		12.34	4.32	35.2	20.5
PI542687	2.28	0.40		18.2	9.9		3.96	2.73	52.7	28.1
PI542688	3.59	0.88		18.0	9.9		4.78	2.24	55.8	23.6
PI542689	3.40	0.78	1.48	16.9	10.8	17.5	4.32	2.80	48.5	31.7
LSD	0.94	0.8		3.4	1.8	3.1	14.28	1.11	9.2	7.7
Mean	3.74	1.19		16.4	11.7		5.38	3.26	52.6	31.6

For each trait, mean values under drought in Spain are presented in the third column

sensitivity or the poorest adaptation. ASI is a clear indicator of drought tolerance at flowering (Bolaños and Edmeades 1996), and the combined effect of drought and adaptation extraordinarily increased ASI for PI527477, PI542683 and PI542687. In a previous report with another set of maize populations from the Sahara, Djemel et al. (2012) also reported that they were able to grow and produce grain under normal conditions in Pontevedra, though some of them had abnormal growth and delayed flowering.

The Algerian populations PI527467 and PI527474 had as vigorous young plants as the adapted checks,

and PI527476, along with PI527469, were as early as the earliest check. The earliest population was not even affected by drought at flowering time. Comparison of ranks under control and stress is an estimator of tolerance; PI542684 and PI542685 had the largest ASI under control and the shortest one under drought, indicating that they were drought tolerant at flowering stage. Algerian populations PI527474, PI527475, PI527478, and PI542684 improved their ranks for plant height under drought conditions, indicating that they had some drought tolerance, besides fair adaptation.

Concerning yield and yield components, PI542688 improved its rank for prolificacy under drought conditions. Among the Algerian populations that were able to produce grain under drought conditions in Spain, the populations PI527470, PI527473, PI527474, PI527472, and PI542683 had medium yield under control conditions and were among those with the highest yield under drought. Mean grain yield reduction caused by drought was around 68%, which is similar to that reported in previous studies (Ertiro et al. 2017; Djemel et al. 2019); but some populations had lower yield reduction in northwestern Spain, indicating that they could be valuable sources of drought tolerance for temperate environments.

Finally, PI527467 and PI527472 improved their ranks for stover yield under drought conditions compared to control conditions and PI527474, PI527475, and PI527478 improved their ranks for stover moisture under drought compared to control conditions. Grain and stover yields followed clearly different patterns not only because poorly adapted populations produced biomass but also because of photoperiod sensitivity that affected grain production more than stover yield.

Therefore, most of the Saharan populations showed some drought tolerance at one or more traits, namely PI527467 for early vigor and stover yield, PI527474 for early vigor, plant height, grain yield and stover moisture, PI527476 for earliness, PI542684 for ASI and plant height, PI542685 for ASI and stover yield, PI527475 for plant height and stover moisture, PI527478 for plant height, stover yield and moisture, PI542688 for prolificacy, PI527470, PI527473 and PI542683 for grain yield, and PI527472 for grain yield and stover yield. Djemel et al. (2019) identified PI527476 as drought tolerant at germination in vitro, PI542685 as drought tolerant at seedling stage in vitro, and PI527473 and PI527474 as high yielders in a preliminary field trial under drought conditions. Although grain and stover yield are the main agronomic criteria, germination is the first limiting factor for drought tolerance (Khodarahmpour 2012; Liu et al. 2015). Djemel et al. (2019) also identified PI542678 among the most drought-tolerant populations with high final germination, more secondary roots and positive Water Use Efficiency. However, PI542683 had also a high ASI, and PI542684 and PI542685 were not completely adapted to northwestern Spain.

As conclusion, adaptation of this semitropical maize germplasm from the Sahara to temperate areas is adequate for incorporation to breeding programs. Therefore, the Algerian maize populations could be considered as an appropriate source for drought tolerance for temperate environments, particularly PI527474, PI527478, PI527472, PI527467, PI527470, and PI527473. Concerning stover yield, the most interesting populations are PI527467, PI542685, PI527478, and PI527472. These Saharan populations could provide favorable alleles for drought tolerance in breeding programs, and could also be used for finding interesting quantitative trait loci under extreme conditions.

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Author contribution AD, OM, and PR designed the experiments. OM and AD performed the experiments in Algeria. LA and PR performed the experiments in Spain. AD and RM analyzed the data. OM and PR wrote the paper. All authors read and approved the manuscript.

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